What Makes Orangutans Intelligent?

The Role of Experience and Learning in the Development of Problem-Solving Abilities in Orangutans

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ABSTRACT

The origins of intelligence and its developmental construction are the subject of on-going debate in evolutionary biology. Humans have remarkable cognitive abilities, as illustrated by our general intelligence, which goes hand in hand with an unmatched brain size relative to body size. But it is not just humans that are special in that sense: primates in general have evolved remarkably large relative brain size. This raises questions about the selective advantages of increased brain size, especially since large brains are not only energetically costly, but their cognitive development requires precious time and practice for maturation. The costs of maintaining a large brain and higher cognitive processes could be a driving factor in cognitive evolution. Whether there is a possible evolutionary continuity of intelligence among primates is still in debate. In order to improve our understanding of the evolution of primate cognition we must disentangle the factors shaping the development of cognitive abilities, including identifying the influences shaping problem-solving mechanisms, in humans and other primates. Especially studies in great apes, our closest living relatives, might lead to novel insights into the factors shaping the development of intelligence and the selective pressures driving the evolution of cognition, and so explain the adaptive significance of intelligence during primate evolution.

With this PhD thesis, I aimed to investigate the determinants of orangutans' cognitive performance and the possible presence of domain-general cognition in the genus *Pongo*. The first empirical chapter investigates the influences of variation in experience during development as a result of variation in rearing background and human contact on the outcome of exploration and cognitive performance in orangutans. With my colleague Dr. Sofia Forss, I compared the influences of developmental conditions and the duration of human exposure between individuals housed in rehabilitation stations and zoological gardens. The data reveals that orangutans experiencing contact with humans during infancy have a different orientation towards humans and express fundamental psychological changes in their problem-solving approach and abilities. This change specifically increases their motivation to explore as well as the duration and variety of their exploration and consequently affects their cognitive understanding of the physical problem-solving task. This finding suggests that in comparison to wild conditions, where individuals show high neophobia, early exposure to humans and our artifacts in captivity produces a broader range of opportunities for learning and exploration, resulting in increased interest and innovativeness. Therefore human-related histories should always be taken into account in standardized cognition tests across primates.

In the next chapter, I expanded the investigation of how an individual orangutan's interest in the social and physical environment affects the developmental construction of its problem-solving ability. I examined an individual's response-and-exploration style, as well as its effects on cognitive

abilities, by measuring its responses to novelty and exploration, and related it to its orientation towards humans. The results revealed curiosity (of which the human orientation in the previous chapter is one element) as the main explanatory factor for the outcome of cognitive performance on five different physical cognitive problem-solving tasks. This striking effect of curiosity was quite unexpected because the genus *Pongo* is known to be very conservative in the wild: individuals avoid novelty and their exploration is almost exclusively socially induced. However, human contact early in life, with the safe and stable living conditions this provides, can unleash orangutan curiosity, which presumably changes an individual's approach to its surroundings and therefore leads to different experiences. What is impossible to imagine for wild orangutans becomes prominent in captivity: a curious life style strongly enhances problem-solving performance and shapes cognitive abilities and understanding. Our ability to unleash this innate potential of curiosity in orangutans provides insight in the factors driving the construction of intelligence, especially the role of experience in this process. These results not only explain why captive primates appear to be so much more intelligent than their wild counterparts (the captivity effect), but may also have important implications for how we explain the dramatic increase of intelligence in our own lineage. When curiosity was added to the mix of factors affecting innovativeness, it may have given a major, so far unappreciated boost to our ancestors' material culture that cannot be explained by changes in brain size and demography. The birth of curiosity may therefore have strongly contributed to making humans behaviorally modern well after we became so morphologically.

The final chapter deals with the question whether orangutans possess domain-general cognitive abilities; in other words it examines the degree to which performance on different cognitive tasks are inter-correlated. There is extensive evidence for a general factor *g* in humans, measured via psychometric analysis and often interpreted as an expression of general intelligence. In order to investigate if there is evolutionary continuity in general intelligence among primates, I thoroughly investigated the presence of *g* in a sample of 53 orangutans, analogous to the psychometric evidence of *g* in humans. Principal component analysis of performance in various carefully selected physical cognitive tasks (each designed to represent different cognitive domains, such as reversal learning and causal reasoning) yielded a first component explaining about a third of the overall variance in the data. This result constitutes the first empirical evidence consistent with *g* in orangutans and comparable to the one found in humans. I found no support for the possibility that this conclusion could be due to confounding effects. I also looked for influences of experiential effects, such as curiosity, and found that there was a strong positive link between curiosity and *g*. Therefore, the factor of curiosity and the effect of individual's experiences during lifetime play a crucial role in the development of stronger cognitive abilities, including domain-general cognitive abilities. By providing solid evidence for the presence of *g* in orangutans, I suggest evolutionary continuity of domain-general cognitive abilities between humans and great apes. This finding thus supports the idea that among primates general intelligence is a phylogenetically old phenomenon.

Overall, my PhD thesis identified important developmental determinants about what makes an orangutan intelligent and shows how these influences might have molded the evolution of intelligence in primates.

ZUSAMMENFASSUNG

Der Ursprung und die Entwicklung der Intelligenz sind Gegenstand des aktuellen Diskurses in der Evolutionsbiologie. Der Mensch hat bemerkenswerte kognitive Fähigkeiten, wie durch unsere allgemeine Intelligenz veranschaulicht wird. Diese geht Hand in Hand mit einer im Verhältnis zur Körpergröße unvergleichlichen enormen Hirngröße. Aber es sind nicht nur Menschen, die in diesem Sinne besonders sind: Primaten haben im Allgemeinen eine erstaunlich relativ große Hirngröße entwickelt. Dies wirft Fragen zu den selektiven Vorteilen der Gehirngröße auf, zumal große Gehirne zum einen nicht nur energetisch kostspielig sind, sondern ihr kognitiver Reifungsprozess auch kostbare Zeit und aufwendiges Training erfordert. Die Kosten für die Aufrechterhaltung eines großen Gehirns mit höheren kognitiven Prozessen könnten ein treibender Faktor für die kognitive Evolution sein. Es stellt sich auch die Frage, ob die Intelligenz unter Primaten möglicherweise evolutionär kontinuierlich ist. Um die kognitive Evolution unter Primaten zu verstehen, müssen wir jene Faktoren erkennen, welche die Entwicklung der kognitiven Fähigkeiten beeinflussen. Das schließt die Identifizierung von möglichen Einflüssen auf Problemlösungsmechanismen bei Menschen und anderen Primaten ein. Insbesondere Studien an großen Menschenaffen, unseren nächsten lebenden Verwandten, können zu neuen Erkenntnissen hinsichtlich solcher Faktoren führen, die die Entwicklung der Intelligenz und den selektiven Druck zur Evolution der Kognition beeinflussen. Auf diese Weise lässt sich die adaptive Bedeutsamkeit von Intelligenz während der Primatenentwicklung untersuchen.

Das Ziel der vorliegenden Doktorarbeit bestand in der Untersuchung der Bestimmungsfaktoren, die die kognitiven Fähigkeiten von Orang-Utans formen und in der Erforschung eines möglichen Vorkommens bereichsübergreifender Kognition (domain-general cognition) in der Gattung *Pongo*. Im ersten empirischen Kapitel werden die Einflüsse verschiedener Erfahrungen in der Entwicklungsphase der Orang-Utans auf die Auswirkung des Explorationsverhaltens und die kognitiven Fähigkeiten untersucht, die durch die individuellen Hintergründe des Aufwachsens wie zum Beispiel dem Kontakt zu Menschen unterschiedlich ausgeprägt sind. Gemeinsam mit meiner Kollegin Dr. Sofia Forss habe ich die Einflüsse von Bedingungen während der Entwicklung und die Dauer der menschlichen Einwirkung zwischen den in Auswilderungsstationen lebenden Individuen und weiteren Individuen aus zoologischen Einrichtungen verglichen. Die Resultate legen dar, dass Orang-Utans, die während ihrer Kindheitsphase Kontakt zu Menschen hatten, eine andere Ausrichtung auf den Menschen zeigen. Die Orang-Utans weisen zudem einen fundamentalen psychologischen Wandel in ihren Problemlösungsstrategien und -fähigkeiten auf. Insbesondere bewirkt dieser Wandel einen Anstieg ihrer Explorationsmotivation sowie der Dauer und Variation ihrer Exploration, so dass ihr kognitives Verständnis für physische Problemlösungsaufgaben beeinflusst wird. Hieraus kann geschlossen werden, dass völlig gegensätzlich zur stark ausgeprägten Neophobie von in freier

Wildbahn lebenden Individuen, in Gefangenschaft lebende Orang-Utans eine frühe Einwirkung von Menschen und unseren Artefakten erfahren, die eine große Auswahl an Gelegenheiten zum Lernen und Explorieren bieten. Dies kann ein erhöhtes Interesse und größere Innovationsfreude bei den Individuen hervorrufen. Diese kulturellen Einflüsse sind für das Verständnis des zugrundeliegenden evolutiven Mechanismus sehr bedeutsam und daher sollten die auf Menschen bezogenen Hintergründe bei standardisierten Kognitionstests mit Primaten stets berücksichtigt werden.

Im anschließenden Kapitel richte ich den Fokus meiner Forschungsarbeit auf die Frage, wie sich das individuelle Interesse eines Orang-Utans an seinem sozialen und physischen Umfeld auf seine Entwicklung von Problemlösungsfähigkeiten auswirkt. Von jedem Individuum untersuchte ich den persönlichen Reaktions- und Explorationsstil sowie deren Auswirkungen auf die individuellen kognitiven Fähigkeiten. Dies erfolgte mit Hilfe von Messungen ihrer Reaktionen und ihre Art der Exploration mit unbekannten Objekten, welche in Verbindung mit ihrer individuellen Ausrichtung auf den Menschen gebracht werden konnte. Die Ergebnisse zeigen, dass Neugierde (als ein Bestandteil der im vorherigen Kapitel beschriebene Ausrichtung auf Menschen) der wichtigste Erklärungsfaktor für das Ergebnis der kognitiven Leistung in fünf verschiedenen physischen kognitiven Problemlösungsaufgaben ist. Diese bemerkenswerte Wirkung der Neugierde ist ziemlich unerwartet, da die Gattung *Pongo* dafür bekannt ist, sich sehr konservativ in der Wildnis zu verhalten: Individuen vermeiden Neuheiten und die Erforschung von Neuem ist fast ausschließlich sozial bedingt. Früher menschlicher Kontakt, durch den sichere und stabile Lebensbedingungen geschaffen werden, kann die Neugierde in Orang-Utans zur Entfaltung bringen, so dass sich dadurch vermutlich die Herangehensweise/Einstellung eines Individuums zu seiner Umgebung verändert, dies führt wiederum zu unterschiedlichen Erfahrungen. In Gefangenschaft bildet sich heraus, was für wilde Orang-Utans nicht vorstellbar ist: Ein neugieriger Lebensstil verbessert die Problemlösungsfähigkeiten und prägt sowohl die allgemeinen kognitiven Fähigkeiten als auch das Problemverständnis. Unser Vermögen das angeborene Potential der Neugierde in Orang-Utans zu entfalten, gibt Einblick in die treibenden Faktoren für den Erwerb und die Entwicklung von Intelligenz, vor allem darüber welche Rolle gesammelte Erfahrungen in diesem Prozess spielt. Diese Ergebnisse erklären nicht nur, warum gefangene Primaten so viel intelligenter zu sein scheinen als ihre wilden Pendants (der captivity-effect), sondern sie könnten auch wichtige Implikationen dafür liefern, wie wir den dramatischen Anstieg an Intelligenz in unserer eigenen Stammeslinie erklären. Neugierde könnte zu einer Mischung aus Faktoren hinzugekommen sein, die Innovationsfähigkeit beeinflussen. Dies könnte zu dem erheblichen und bisher nicht gebührend gewürdigten Schub in der materiellen Kultur unserer Vorfahren geführt haben, der nicht allein durch Hirngröße und Demographie erklärt werden kann. Die Entstehung der Neugierde könnte daher maßgeblich dazu beigetragen haben, dass der Mensch verhältnismäßig modern wurde, lange nachdem wir morphologisch zu Menschen wurden.

Im abschließenden Kapitel geht es um die Frage, ob Orang-Utans bereichsübergreifende (domain-general) kognitive Fähigkeiten besitzen; es wird - mit anderen Worten - untersucht, inwieweit die Leistungen verschiedener kognitiver Aufgaben interkorrelieren. Innerhalb der Menschen gibt es umfangreiche Belege für einen Generalfaktor der Intelligenz *g*, der über psychometrische Analysen gemessen wird und oft als Ausdruck der allgemeinen Intelligenz interpretiert wird. Um zu untersuchen, ob es eine evolutionäre Kontinuität in der allgemeinen Intelligenz unter Primaten gibt, untersuchte ich das Vorhandensein von *g* in einer Stichprobe von 53 Orang-Utans, analog zur Anwendung des psychometrischen Nachweises von *g* beim Menschen. Die Hauptkomponentenanalyse der Leistungen von verschiedenen, sorgfältig ausgewählten physischen kognitiven Aufgaben (die jeweils unterschiedliche kognitive Bereiche repräsentieren, wie Umkehrlernen und kausales Schlussfolgern) ergab eine erste Komponente, die ein Drittel der Gesamtstreuung der Daten erklärte. Dieses Ergebnis stellt den ersten empirischen Hinweis für *g* in Orang-Utans dar, das vergleichbar ist mit dem beim Menschen gefundenen *g*. Ferner fand ich keine Hinweise für die Möglichkeit, dass die allgemeine kognitive Leistung der Orang-Utans ein Artefakt aus Störfaktoren sein könnte. Ich suchte auch nach Anzeichen für die Auswirkung von Erfahrungen, wie Neugierde, und konnte einen starken positiven Zusammenhang zwischen Neugierde und *g* feststellen. Daher spielen der Faktor Neugierde und die Auswirkungen der individuellen Erfahrungen während der Lebenszeit eine entscheidende Rolle bei der Entwicklung stärkerer kognitiver Fähigkeiten, einschließlich bereichsübergreifender allgemeiner kognitiver Prozesse. Aufgrund der vorliegenden starken Anzeichen für die Existenz von *g* in Orang-Utans schlage ich eine evolutionäre Kontinuität von bereichsübergreifenden kognitiven Fähigkeiten zwischen Menschen und großen Menschenaffen vor. Dieser Befund stützt die Idee, dass allgemeine Intelligenz ein phylogenetisch altes Phänomen unter Primaten ist.

Zusammenfassend beschäftigt sich meine Dissertation mit der Frage *Was macht einen Orang-Utan intelligent?*, indentifiziert wichtige Entwicklungsdeterminanten für kognitive Fähigkeiten und legt dar, wie diese Einflüsse die Evolution der Intelligenz in Primaten geprägt und geformt haben könnten.

General Introduction

GENERAL INTRODUCTION

How and why do humans differ from other animals and especially from great apes? Philosophers, theologians, psychologists and anthropologists have discussed these questions since ancient times and produced an array of hypotheses and theories (Kappeler and Silk 2010, van Schaik 2016). Undoubtedly, the drive to understand our own species' evolutionary origins as well as the presence of striking differences of mind, behaviour and life history compared to other primate species and other nonhuman animals has motivated much research, and continues to do so. Numerous comparative studies on humans and great apes show similarities between the species that suggest a long shared evolutionary continuity of many traits. Still, our unmatched large brains in relation to body-size, which go in hand with remarkable cognitive abilities, including general intelligence, are subject to on-going studies about their evolutionary origins and comparative investigations in primatology research, especially of great apes, our closest living relatives.

Defining Intelligence

Before reviewing the literature on the evolution of intelligence and important influences that possibly shape cognitive processes, it is necessary to define cognitive abilities, domain-specific versus domain-general abilities, and intelligence.

Cognition refers to all mental processes (involving the brain) that include the acquisition, processing and storage of information and are therefore involved in producing behavioral actions. A more narrow definition includes only those mental processes that involve some form of mental representation (Tomasello and Call 1997, van Schaik 2016). These latter *cognitive processes* are especially called for when dealing with novel ecological and social situations (novel problems) (Mayer 1992, Mayer and Wittrock 2006) and the individual itself has to find a new way (solution) to overcome these challenges. Therefore, *cognitive abilities* are related to *problem-solving abilities*. It is difficult to directly measure cognitive abilities in any given species, but by measuring the *problem-solving skills* of an individual, it is possible to refer from there to the inherent cognitive potential, thus the underlying ability (Burkart et al. 2009).

It is generally assumed that the mind of animals that show higher cognitive abilities are adapted to their very specific environment through *domain-specific abilities* or *modules* (Duchaine et al. 2001). Human cognition also includes such domain-specific components (Cosmides and Tooby 2013). These specialized cognitive mechanisms or adaptive specializations are genetically based and developmentally canalized solutions that evolved to deal with very specific adaptive problems (Duchaine et al. 2001, Cosmides and Tooby 2002, Burkart et al. 2017) and cannot be applied in different context (i.e. across domains). Therefore the 'solutions' to the specific problems are fixed and show no flexibility and no effects of experience through learning on performance.

In contrast to *domain-specific abilities,* the *domain-general abilities*, such as learning or behavioral flexibility, function across multiple domains and contexts and form the basis of intelligence. For humans *intelligence* can broadly be defined as the abilities of reasoning, problem-solving, abstract thinking, planning, comprehension and learning from experience (Gottfredson 1997). It can be measured via psychometric, factor-analytical approaches that yield one main factor across different tasks and domains, independent of content (Johnson et al. 2004), the general factor *g* (Spearman 1904, 1927, Carroll 1993, Jensen and Weng 1994, Jensen 1998, Hunt 2011). This general ability of intelligence, as it was first proposed by Spearman (1904), was later subdivided by Cattell into two distinct sub-ordered abilities: *crystallized intelligence* and *fluid intelligence* (Cattell 1963, Horn and Cattell 1966, Horn 1968, Geary 2005, Blair 2006, Horn and McArdle 2007). Whereas crystallized intelligence refers to the stored knowledge and skills that have been acquired during lifetime via learning and experience, fluid intelligence describes the underlying abilities that make it possible to acquire knowledge and skills, such as instantly solving novel problems and using inductive reasoning (Jensen 2002). Especially the ability to flexibly learn new information during lifetime is associated with fluid intelligence (Cattell 1971, Ackerman 1986, 1988).

For animals, *intelligence* is not as broadly defined, but it is also clear that intelligence is not about biologically constrained learning of very specific solutions, but instead means the acquisition of knowledge, behavioral flexibility and problem solving in both familiar and novel environments (Byrne 1994, Yoerg 2001, Rumbaugh and Washburn and Washburn 2003).

There are numerous examples showing that the behavioral reactions of animals are not fixed, but that they respond to changes in social and ecological situations with new behaviour patterns or modifications of their existing behavior patterns (Kummer and Goodall 1985, Lefebvre et al. 1997, Reader and Laland 2001, 2003). Thus, just as in humans, the core features of intelligence in nonhuman animals are the acquisition of knowledge (learning ability) and problem-solving in novel context (Byrne 1994, Yoerg 2001, Rumbaugh and Washburn and Washburn 2003).

When aiming to test cognitive abilities and intelligence in any species, one has to carefully design the test-batteries to avoid confounding measurements. Importantly, there is no culture-free testing, since social-cultural experiences during ontogeny influence the way intelligence is developed in all species studied to date (see section ***Development of Intelligence***).

Evolution of Intelligence

The evolution of intelligence is directly linked to an evolutionary increase in relative brain size (encephalization). Higher cognitive processes, such as flexible learning, are related to enlarged brains (Byrne and Whiten 1988, Harvey and Krebs 1990, Dunbar 1995, Byrne 1997, Reader and Laland 2002, Lefebvre et al. 2004, Deaner et al. 2007, Burkart et al. 2017). Especially the domain-general cognitive abilities are thought to require additional brain tissue (Deaner et al. 2007, Reader et al. 2011). Large

brains, however, are known to be energetically very costly (Rolfe and Brown 1997, Geary 2005, Bauernfeind and Babbitt 2014, Kuzawa et al. 2014). They require a stable energy supply to be maintained (Mink et al. 1981, Holliday 1986, Navarrete et al. 2011). In spite of these costs, some species, such as primates, have nonetheless evolved large brains and with it advanced cognition and general cognitive flexibility (Deaner et al. 2007, Reader et al. 2011), implying that the benefits of having a larger brain must have outweighed the costs (Isler and Van Schaik 2014). This raises questions about the influence of ecological and social factors driving the evolution of encephalization, and how the costs of developing larger brains can be outweighed by the adaptive benefits of higher cognitive abilities.

It is commonly thought that group living, with its social restrictions and challenges, drove the evolution of enhanced cognitive abilities (*the Social Brain Hypothesis*, Byrne and Whiten 1988, Dunbar 1998). Especially the cognitively demanding dynamics of social bonding and coalitions (Dunbar and Shultz 2007) or the improved effectiveness of social transmission (e.g. Whiten and van Schaik 2007, Pradhan et al. 2012) were thought to be important for the evolution of intelligence. In addition, ecological factors were suggested to have acted as selective pressures driving the evolution of enlarged brains. Needing to maximize a stable energy income through the fluctuating year, individuals not only have to be behaviorally flexible to prevent experiencing food scarcity (*the Cognitive Buffer Hypothesis*: Allman et al. 1993, Deaner et al. 2003; Sol 2009a,b), but also require special techniques and higher levels of cognition for the extraction and processing of difficult to acquire food (*the Technical Intelligence Hypothesis,* Byrne 1997, Parker and Gibson 1977).

More recent primate research on brain size evolution, which combines the ecological and social preconditions, clearly shows that mainly ecological preconditions favored the evolution of large brains, not the social ones (Graber et al. in prep). However, lineages that had favorable ecological conditions that drove encephalization could also develop enhanced cognitive abilities in the social domain. The evidence of correlated evolution of socio-cognitive and eco-cognitive abilities found by Graber et al. (in prep.) strongly suggests the presence of domain-general cognitive abilities. Obviously, there is also overlap between the ecological and social domains: Once a particular set of social skills, such as social learning, has evolved it might indirectly favor the evolution of enlarged brains by improving the access and energy intake of important food resources. This hypothesis can be applied to the evolution of intelligence, but also be applied developmentally: conditions favoring learning and experiences during ontogeny most likely shape an individual's development of cognitive abilities.

Development of Intelligence

The importance of learning

Proficient problem-solving abilities and cognitive understanding of ecological challenges are thought to be advantageous for an individual and lead to fitness benefits in demanding environments. However, species that show higher cognitive capacities are not born intelligent, but rather train and

mature their cognitive abilities during ontogeny via learning through experiences (Wilson 1991, Reader and Laland 2002, Whiten and van Schaik 2007, van Schaik and Burkart 2011, Galef 2015). There is a genetic foundation for intelligence (for humans: Neisser et al. 1996, Bouchard 2004, Deary et al. 2009, Davies et al. 2011, Nisbett et al. 2012, Bates et al. 2013, Joshi et al. 2015, for chimpanzees: Hopkins et al. 2014, for mice: Galsworthy et al. 2005), in particular the ability to learn (Rumbaugh and Washburn and Washburn 2003). Although this forms the genetic basis for the construction of intelligence, it is subsequently critically dependent on social and environmental inputs during development (for humans: reviewed in Neisser et al. 1996, reviewed in Nisbett et al. 2012).

The importance of learning becomes even clearer when bringing the consequences of enhanced learning abilities to mind (Figure 1): Through learning, the individual can gather knowledge and increase its set of learned skills important for survival. Natural selection after all acts on the individual's skill sets relevant for survival, i.e. the products of learning, and not learning ability per se. In particular, the ability of social learning can be used as a crucial tool. Social learning enables the individual to learn from other individuals, which was shown to be faster than individual learning and connected to fewer risks; in other words: social learning is simply more efficient than asocial learning (van Schaik and Burkart 2011). Additional, through social learning the knowledge of skills of the population can be transmitted not only horizontally, but also vertically between generations. Depending on the environment and the size of the population's skill pool, the opportunities for social learning may play an important role in determining the content of an individual's skill set. Especially in demanding environments with varying conditions, the socially acquired knowledge of hidden food resources and extracting foraging techniques can be a major advantage.

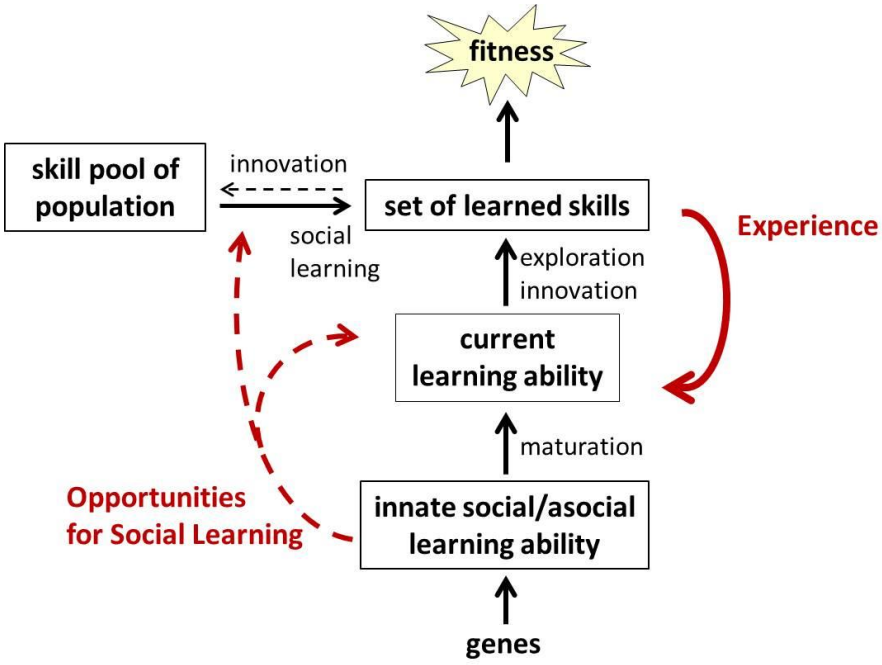

Figure 1: Genetic, social and environmental impacts on intelligence – the cultural intelligence hypothesis. Graphic adapted from van Schaik and Burkart (2011).

Influences of the social environment during ontogeny therefore play crucial roles for developing cognitive abilities. They define the conditions under which learning takes place, determine the scope of individual's actions and responses towards the situation, and shape the array of skills to be learned. The Cultural Intelligence Hypothesis describes how influences of the social-cultural environment during development shape the cognitive abilities and the set of learned skills of an individual (Figure 1) (Tomasello 1999, Herrmann et al. 2007, Whiten and van Schaik 2007, van Schaik and Burkart 2011). What was first suggested to explain the development of uniquely human cognitive abilities (Tomasello 1999, Herrmann et al. 2007), was later also proposed for nonhuman animals (Whiten and van Schaik 2007, van Schaik and Burkart 2011). The cultural intelligence hypothesis predicts that in a stimulating social-cultural environment with increased opportunities for social learning, individuals will develop lager skill repertoires and minds capable of better cognitive performance on a developmental, but also on an evolutionary level (van Schaik and Burkart 2011, van Schaik 2016). This idea was recently confirmed for orangutans (Forss et al. 2016). When comparing it to Cattell's model of intelligence, the knowledge and learned skills are referring to crystallized intelligence, whereas the underlying current learning ability can be compared to fluid intelligence. Under stimulating external conditions, these two forms of intelligence will therefore show a strong positive correlation.

The role of experience

Learning means gaining knowledge and experience, which means that the content depends strongly on the environment. The more opportunities the learning environment offers, the greater the set of learned skills an individual acquires (through social or asocial learning) and the more knowledge of affordances through experience the individual gains (Fig. 1). This affects the current learning ability, regardless of how this knowledge was learned (socially or asocially). This experience effect is possible because both abilities of social and asocial learning share similar underlying cognitive mechanisms (Heyes 1994, Heyes 2012). It is a cumulative process shaping the way individuals approach, explore and understand their world, and thus influences the quality and quantity of opportunities for learning. Obviously, in this positive-feedback process it matters how an individual approaches its environment, deals with novel situations and interacts with social, but also asocial opportunities for learning.

Especially in the absence of a social learning partner, the approach to a stimulus is very important for a learning experience – in order to be able to explore, the individual must approach the resource (Greenberg and Mettke-Hofmann 2001, Reader and Laland 2003). Therefore, an individual's approach and response style can be of great importance for learning, exploration and developing cognitive abilities. It has been shown that reduced neophobia was correlated with better problem-solving skills in nonhuman animals (Auersperg et al. 2011, Benson-Amram and Holekamp 2012, Sol et

al. 2012, Cauchard et al. 2013): Individuals that are more prone to novelty seeking have a different attentiveness toward their environment, may more easily recognize learning situations and might explore their environment differently. In chimpanzees (Hopper et al. 2014) and capuchin monkeys (Morton et al. 2013) an individual's temperamental openness (to experience) is correlated with successful responses towards a novel problem-solving task. It might therefore be possible that motivational aspects and curiosity underlie learning and innovation processes (Reader and Laland 2003). The tendency for exploration may often be intrinsically self-rewarding, because individual exploration is sometimes observed in the absence of any direct reward ('intrinsic' exploration: Harlow et al. 1950, Thorpe 1956, McFarland 1981, Archer and Birke 1983, Reader and Laland 2003). The mere presence of a novel stimulus can sometimes elicit a 'curious' response in humans (Berlyne 1950). All of these above-mentioned relations have to be investigated more closely to better understand the influencing factors and the role of learning and experience for the development of cognitive abilities. So far, little is known about the internal motivational factors influencing cognition, their interrelation to external conditions and the overall effect on behaviour and problem-solving skills.

Socio-cultural effects and environmental conditions during development significantly shape the behaviour, experiences and eventually cognitive abilities of an individual: Long lasting effects of rearing and environmental conditions have been documented for primates, especially in two extreme cases, deprivation and enculturation. Captive individuals that grow up in a more stimulating socio-cultural environment show more rapid behavioral and motor development, increased number of learned skills, more sophisticated object manipulation and more skillful tool use (rev. in van Schaik and Burkart 2011, rev. in Björklund 2006, rev. in Call and Tomasello 1996, Tomasello and Call 2004, Gardner and Gardner 1989, Bard and Gardner 1996, Fredman and Whiten 2008, Furlong, Boose and Boysen 2008). In contrast, studies during which primates are deprived of stimulating environmental or social enrichment show the opposite effects. Early maternal separation seems to lead to reduced socio-cognitive abilities (Gilmer and McKinney 2003). Individuals deprived of environmental inputs show reduced competence in many physical skills, e.g. nest building (Videan 2006), tool use (Menzel Jr et al. 1970, Morimura and Mori 2010), and a smaller set of learned skills (rev. in van Schaik and Burkart 2011, Ruppenthal et al. 1976). Whilst studies on deprivation and enculturation certainly are of great value for our understanding of how intelligence evolved in large brained species, within-species variation in cognitive performance exists beyond these two extremes. Moreover, these studies do not reveal the processes involved in producing these outcomes.

Even subtle variation in opportunities for learning and variation in experiences during development beyond the species-typical repertoire might lead to changes in behaviour and learning. This is most evident when comparing captive versus wild individuals of the same species. In captivity, the reduced overall risk, increased free time and increased social interaction, including contact with humans, were suggested to underlie the increase in exploration and cognitive abilities, a phenomenon commonly known as the captivity effect (Laidre 2008, Benson-Amram et al. 2013, Forss et al. 2015). The exposure to humans and their artifacts offer broader exploration opportunities (Russon and

Galdikas 1993, Byrne and Russon 1998, Shumaker et al. 2011). According to the Cultural Intelligence Hypothesis, these opportunities for learning can change the knowledge and skill repertoire of an individual, explaining variation in problem-solving performance. Increased contact with humans can additionally change the social understanding of individuals: usually primates perform very poorly at locating hidden food using social cues and social-communication from humans. However, individuals that grew up with humans perform far better (Anderson et al. 1995, Call et al. 2000, Lyn 2010).

The developmental construction of intelligence has consequences for how we think about its evolution. Little is still known about the interaction between factors influencing the individual's style of approach, response and exploration of previously unexplored features of the environment, leading to differences in opportunities for learning, which in turn shape the knowledge and skill repertoire of an individual. This provides selection with a great number of variables to act upon. Especially because we not only find between-, but also within-species variation in cognitive performance, the study of developmental influences might lead to insight in the selective pressures driving the evolution of cognition. It is therefore very important to investigate the developmental conditions that favor learning abilities, behavioral flexibility, and cognition during development. This is most promising in nonhuman primates, our closest relatives.

Orangutans as a model species for Intelligence

Orangutans in the wild and captivity show great cognitive plasticity and are known to be very good problem solvers (Lethmate 1977, Lehner et al. 2011). A systematic investigation of individual variation in orangutans' cognitive performance will thus most likely significantly increase the understanding of the evolution of primate intelligence.

First, the genus *Pongo* with its two subspecies *Pongo pygmaeus* on the island of Borneo and *Pongo abelii* on Sumatra is one of our closest living relatives, with only chimpanzees, bonobos and gorillas being even more closely related to us. The two species shared a common ancestor approximately 0.9–1.1 Ma (Greminger 2015). The evolutionary divergence between orangutans and humans is estimated to have taken place 9-13 million years ago (Hobolth et al. 2011, Prado-Martinez et al. 2013). Although this divergence took lace much earlier than that between hominins and the chimpanzee-bonobo ancestor, orangutans and humans share a variety of traits, such as a long life history, omnivorous ecology with a strong extractive element, and similar basic cognitive abilities (Herrmann, Wobber and Call 2008).

Second, both orangutan species evolved large brains, with Sumatran orangutans relative brain size being slightly larger than that of Borneans (Taylor and van Schaik 2007, van Schaik et al. 2009). This difference is also reflected in their innate problem-solving ability (Forss et al. 2016). In general, their large brains are good preconditions for having general cognitive abilities (Burkart et al. 2017). If we assume evolutionary continuity of general intelligence, orangutans might also possess some level

of domain-general abilities (measured in humans through *g*). In fact, orangutans seem to have all the requirements for having *g* - as suggested for other primate species (Herndon et al. 1997, Banerjee et al. 2009, Hopkins et al. 2014, Woodley of Menie et al. 2015). However, given uncertainties in interpretation and a clear risk that some results represent false positives (Burkart et al. 2017), there is a need for research that assesses the extent of evolutionary continuity of general intelligence, and orangutans are an excellent species for this.

Third, orangutans live in an environment with fluctuating food availability (Marshall et al. 2009). They are specialized in complex food processing techniques that reflect their complex foraging niche (van Schaik et al. 1996, van Schaik et al. 2003, Jaeggi et al. 2010, Schuppli et al. 2012, Schuppli et al. 2016a). However, this knowledge has to be acquired via learning. The mother is an especially important role model (van Noordwijk et al. 2009, Schuppli et al. 2016b). Therefore, like us humans, orangutans are characterized by sophisticated social learning skills (Stoinski and Whiten 2003, Dindo et al. 2010) and the presence of role models during ontogeny for knowledge transfer (Jaeggi et al. 2010, Schuppli et al. 2016b). As a result, behavioral variation between populations qualifies as cultural variation (van Schaik et al. 2003, van Schaik et al. 2009, Krützen et al. 2011).

Fourth, intraspecific variation in behavior, novelty response and cognitive abilities were found between wild and captive orangutans (Forss et al. 2015). Still, little is known about the influences of socio-cultural- and housing conditions on the cognitive abilities and problem-solving mechanisms under non-extreme conditions. Orangutans with their slow development (Wich et al. 2004, Wich et al. 2009), socially learned skill repertoires and innate learning competence are ideal to investigate the internal and external influences on cognitive performance.

Fifth, wild orangutans are highly neophobic (Forss et al. 2015). It is very hard to conduct experimental studies in the wild, and almost impossible to conduct cognition-studies under controlled, comparable settings in nature. Consequently, almost all studies investigating orangutans' cognitive abilities and behavioral flexibility were conducted under captive settings, e.g. zoological gardens. However, being born and raised in captivity, these individuals might consequently not show the same abilities as their wild conspecifics. In order to investigate the full range of influences on cognitive performance on a developmental level, individuals with various backgrounds are needed. Therefore, studies that determine different social-cultural influence during ontogeny due to e.g. subtle background differences are needed to investigate what influences during development shape cognition. With this thesis I address these issues to shed light on the evolution of intelligence.

Aims of this PhD dissertation

Examination of the determinants of variation in cognitive abilities within primate species has great potential to provide insight in the factors driving the evolution of brain size and intelligence. With this dissertation, I therefore aim to examine individual variation in cognitive abilities among Sumatran (*Pongo abelii*) and Bornean (*Pongo pygmaeus*) orangutans housed at rehabilitation stations

across Central Kalimantan and Sumatra in Indonesia (Figure 2). By conducting studies with orangutans in rehabilitation stations I had the full advantage of testing individuals that ranged from behaving naturally (i.e. uninterested in humans or even fearful) to very tame, with backgrounds ranging from being wild (with no human influence) to being kept as a human pets for several years. Therefore, the variation in the cognitive performance of these rehabilitant orangutans provides an ideal opportunity to investigate the role of individual experiences and learning during ontogeny for the development of problem-solving abilities and intelligence. This work is important because it allows us to assess the developmental influences that might have shaped the evolution of intelligence as well as the evolutionary continuity of intelligence in primates.

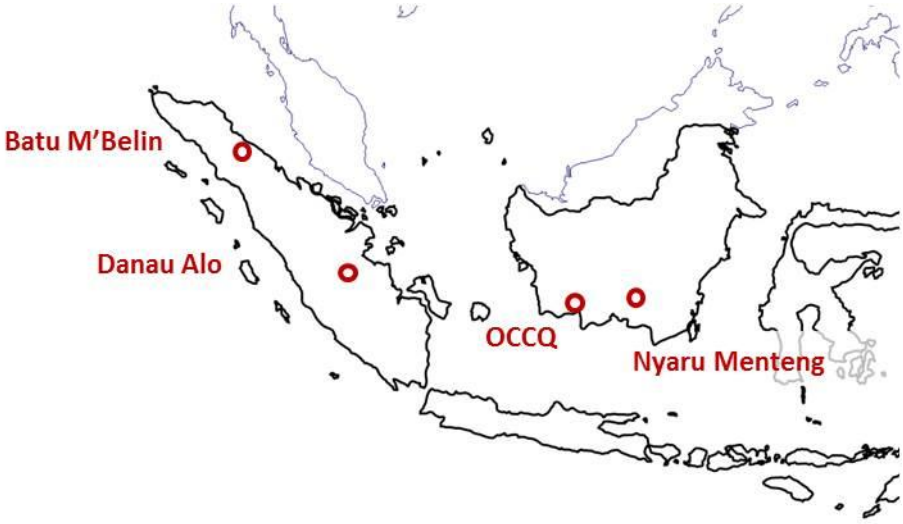

Figure 2: Map of the western part of Indonesia with the locations of the rehabilitation stations on Sumatra (Batu M'Belin and Danau Alo) and Borneo (OCCQ and Nyaru Menteng) marked with red circles.

This dissertation consists of three research chapters that are all based upon the same dataset of up to 61 orangutans living in rehabilitation stations, collected between May 2012 and June 2014. The first two chapters investigate the effects of experience and rearing history on the orangutans' problem-solving approach and their cognitive performance. The third chapter investigates orangutans' cognitive abilities across various task domains and the possible presence of domain-general processes in orangutans.

I. Rearing Background and Human Contact

In the first chapter, I aimed to investigate the effects of social experiences during ontogeny, e.g. contact to humans, on the outcome of orangutan problem-solving abilities. If social learning from role models during the early years enhances cognitive capacities, it is to be expected that individuals with a background of high social contact with conspecifics, and possibly humans, show different and more extensive cognitive abilities than individuals with fewer

opportunities for social learning. In order to generate a large sample of individuals with varying rearing backgrounds and social experiences, I collaborated with my colleague Dr. Sofia Forss; we combined my data on the performance of the rehabilitation station housed orangutans to the identical study she performed on orangutans housed at nine different European zoos and, thus, produced a large data set of 103 individuals. This allowed us to examine the effects of different housing conditions and biographical backgrounds on the development of their problem-solving approach and their cognitive abilities. Previously published research on rearing effects on cognition concerns the social skills of apes, whereas this study was testing a physical cognitive task involving tool-use abilities. In particularly we were interested whether and how different exposure to humans influences explorative behavior, neophobia and cognitive performance in orangutans. Overall, the first chapter gives us an insight in how the social and housing conditions experienced during development, including contact to humans, cause different approaches to problem-solving and intellectual performance.

II. Experiences and problem-solving style

The second chapter of this dissertation addresses the question of how cognitive abilities are determined by an individual's style of problem-solving, in particular the role of curiosity. Earlier studies suggested higher curiosity going along with enhanced problem-solving abilities in captivity. Additionally, my first study of this dissertation (chapter 1) identified an individual's interest in humans to be the major determinant of problem-solving performance in orangutans. The purpose of this second study was to gain broader insight into the nature and causes of interest in the social and physical environment and to further disentangle the effect of curiosity on problem-solving performance. Therefore, in this study, we complemented the first study of orangutan interest in humans (chapter 1) with a multi-dimensional approach that includes both a greater variety of measures of an individual's response-and-exploration style and tests of a number of physical problem solving tasks. This way I could gain novel insights into how curiosity affects an individual's problem-solving approach and further disentangle the various possible contributing factors, e.g. the effects of previous experiences, that gave rise to curiosity.

III. General Intelligence

The purpose of this third chapter was to examine the consistency of orangutans' cognitive performance across different cognitively demanding tasks. There is extensive evidence for across-domain correlations of performance in humans, measured via a general factor *g*, and often interpreted as a measurement of general intelligence. Although intraspecific studies in

nonhuman animal species also report findings on *g*, further validation of these results is desirable. Therefore, the question of evolutionary continuity in domain-general processes shared between human and nonhuman animals remains unresolved and further studies on this topic, especially in primates, are needed. With this third study I primarily aimed to reveal the presence of possible domain-general cognitive processes in orangutans. Importantly, in contrast to most other nonhuman studies on *g*, we aimed to control for alternative non-cognitive factors possibly falsely producing *g*, and to test additional predictions of the presence of *g*, such as pronounced developmental effects and the correlation with social interest. In sum, the purpose of this study was to examine the presence of *g* in orangutans and to link it to biological, social and developmental properties.

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Chapter 1

Orientation toward Humans predicts Cognitive Performance in Orangutans

Orientation toward Humans predicts Cognitive Performance in Orangutans

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Non-human animals sometimes show marked intraspecific variation in their cognitive abilities that may reflect variation in external inputs and experience during the developmental period. We examined variation in exploration and cognitive performance on a problem-solving task in a large sample of captive orangutans (*Pongo abelii* & *P. pygmaeus*, N=103) that had experienced different rearing and housing conditions during ontogeny, including human exposure. In addition to measuring exploration and cognitive performance, we also conducted a set of assays of the subjects' psychological orientation, including reactions towards an unfamiliar human, summarized in the *human orientation index* (HOI), and towards novel food and objects. Using generalized linear mixed models we found that the HOI, rather than rearing background, best predicted both exploration and problem-solving success. Our results suggest a cascade of processes: human orientation was accompanied by a change in motivation towards problem-solving, expressed in reduced neophobia and increased exploration variety, which led to greater experience, and thus eventually to higher performance in the task. We propose that different experiences with humans caused individuals to vary in curiosity and understanding of the physical problem-solving task. We discuss the implications of these findings for comparative studies of cognitive ability.

Introduction

Human intellectual performance is known to be strongly affected by developmental inputs (Bouchard et al., 1990; Neisser et al., 1996; Nisbett et al., 2012). However, similar effects in nonhuman primates have received far less attention. So far, the possible effect of experience on cognitive abilities in nonhuman primates has mainly been studied by examining the two extreme cases of deprivation and enculturation. Physical and social deprivation have been reported to cause strong negative outcomes on cognitive development in primates; especially maternal separation has been shown to result in both short- and long-term socio-cognitive consequences (Davenport, Rogers, & Rumbaugh, 1973; Freeman & Ross, 2014; Gilmer & McKinney, 2003; Gluck & Harlow, 1971; Gluck, Harlow, & Schiltz, 1973; Harlow & Zimmerman, 1959; Kalcher-Sommersguter et al., 2015; Turner, Davenport Jr, & Rogers, 1969). The opposite extreme in rearing environment is enculturation. Especially among great apes, enriched socio-cultural inputs, in the form of extensive interactions with humans, result in enhanced physical cognitive skills (Bard & Gardner, 1996; Furlong, Boose, & Boysen, 2008; Gardner, Gardner, & Van Cantfort, 1989; see also Fredman & Whiten, 2008), but particularly in improved socio-cognitive and communicative abilities (Bjorklund, 2006; Call & Tomasello, 1996; Rumbaugh & Washburn, 2003; Tomasello & Call, 2004; Tomasello, Savage-Rumbaugh, & Kruger, 1993). Both deprivation and enculturation therefore demonstrate that extreme social influences shape the cognitive abilities of nonhuman primates.

Even without being deprived or enculturated, captive primates also show intraspecific variability in cognitive abilities (Herrmann & Call, 2012; Herrmann et al., 2010), but the sources of this variability remain largely unstudied and it remains unclear whether the same social processes are involved. In particular, we don't know to what extent variable rearing histories affect cognitive performance across individuals under non-extreme conditions, and if so whether they do so through their effect on psychological variables such as motivation to solve problems, responses to novelty and exploration style.

The aim of the present study was, first, to examine in a sample of more than 100 captive orangutans (*Pongo abelii* and *P. pygmaeus*) how variation in captive management regimes and individual rearing histories affects psychological variables, such as human orientation, motivation and exploration style, and second, to examine whether these factors explain variation in cognitive performance in a tool-use task. Our sample contained orangutans from a wide range of rearing backgrounds: both zoo groups, including mother- and hand-reared individuals, and individuals housed in rehabilitation stations who were wild-born but subsequently experienced captivity for variable periods of time, some as pets, before entering the rehabilitation station. Importantly, the individuals were all currently kept in captivity, allowing similar individual testing conditions. This provided us with an excellent opportunity to test the strength of the long-term effects of early rearing conditions on exploration styles and cognitive performance.

Because our sample included individuals from both zoos and rehabilitation stations, we could also test the independent effect of current housing conditions. Zoos and rehabilitation stations differ in their purpose of holding captive apes. Zoo apes have lived all their lives in a similar and stable environment, mostly together with their mothers and in intense contact with both knowledgeable conspecifics and human caretakers, with additional exposure to human strangers on a daily basis. Virtually all zoos also offer additional enrichment in the form of various foraging activities. In rehabilitation stations the purpose is very different. Some individuals may have experienced traumatic events in their past (capture and loss of mother, sometimes accompanied by injury) and thus need to recover physically and mentally. The stations' ultimate aim is to return individuals to the wild. They consequently avoid bringing about a too close attachment to humans or exposing them to artificial enrichment devices. Moreover, most rehabilitating apes lack the close bond to their mother and are instead housed in peer groups.

Reactions to an unfamiliar human have previously been used to measure temperament in great apes (Herrmann et al., 2011) and physiological distress responses in monkeys (Kalin & Shelton, 1989; Kalin et al., 1998). In order to estimate the underlying psychological consequences of human-related experiences that might explain variation in exploration and cognitive performance, we developed a new measure, the human orientation index (henceforth: HOI; see Methods for details). This measure was developed because the effect of captivity on cognitive abilities (Benson-Amram, Weldele, & Holekamp, 2013; Laidre, 2008) seems to reflect a major psychological change. First, because in multiple species, reduced neophobia has been shown to influence problem-solving skills (Auersperg et al., 2011; Benson-Amram & Holekamp, 2012; Cauchard et al., 2013; Sol, Griffin, & Bartomeus, 2012), and because captive orangutans show strongly increased interest in novel items relative to their wild counterparts (Forss et al., 2015) (as do other species cf. Benson-Amram, Weldele, & Holekamp, 2013; Visalberghi, Janson, & Agostini, 2003), we assessed the response to novelty across individuals with different captive experiences. Second, because the effect of captivity on cognitive performance is particularly pronounced in the context of tool use (Bentley-Condit & Smith, 2010; Boysen et al., 1999; Hihara et al., 2003; Santos et al., 2006; Lehner, Burkart, & van Schaik, 2011; Shumaker, Walkup, & Beck, 2011), we assessed cognitive performance using a novel tool-use task including multi-step problem-solving with high ecological validity: the honey-tool task. In order to prevent variation in human orientation from confounding cognitive performance during the testing, no humans were present during the tests, which were video-recorded.

Methods

Subjects and study facilities

Our total sample size involved 103 orangutans: 68 *Pongo pygmaeus spp* and 35 *Pongo abelii* (Supplementary Table S6). Data collection on the zoo-housed sample took place at nine different

European zoos between November 2012 and January 2015; all zoo data was collected by SF (Table 1). In total the zoo sample consisted of 41 individuals, of whom 31 were mother-reared and 10 whose own mother had either died or rejected the infant and were therefore hand-reared. They were cared for by human caretakers, within the zoo or partly within a human household, and subsequently returned to a group of zoo-living conspecifics (Table 2).

Table 1: Overview of subjects and facilities

Study Facility	N	Species	Age Range	Social Housing	Test Location	Time Period
Zoo 1	6	*P. pygmaeus*	6-43	Mixed-age group	Sleeping quarter	Apr-May 2013
Zoo 2	8	*P. pygmaeus*	13-52	Mixed-age group	Sleeping quarter	Jan-Feb 2014
Zoo 3	4	*P. abelii*	5-13	Mixed-age group	Smaller enclosure	Nov 2013
Zoo 4	4	*P. pygmaeus*	13-31	Mixed-age group	Sleeping quarter	Jan 2015
Zoo 5	4	*P. abelii*	8-23	Mixed-age group	Sleeping quarter	Nov-Dec 2012
Zoo 6	5	*P. abelii*	9-49	Mixed-age group	Sleeping quarter	Mar 2013
Zoo 7	6	*P. abelii*	5-25	Mixed-age group	Test enclosure	Mar 2014
Zoo 8	2	*P. pygmaeus*	18-20	Mixed-age group	Sleeping quarter	Feb 2015
Zoo 9	2	*P. pygmaeus*	14-36	Mixed-age group	Sleeping quarter	Jan-Feb 2013
Rehab. Station 1	5	*P. abelii*	3-6	Solitary	Home enclosure	Apr-Jun 2013
Rehab. station 2	18	*P. pygmaeus*	6-17	Solitary	Home enclosure	May-Jun 2014
Rehab. station 3	28	*P. pygmaeus*	8-14.5	Peer group	Test enclosure	June-Sep 2012
Rehab. station 4	11	*P. abelii*	5-25	Solitary	Home enclosure	Oct 2012-Mar 2013

Data on 62 rehabilitation orangutans were collected between June 2012 and June 2014 by LD and ZK, supported by a trained assistant, Andreas Wendl. In Borneo data collection took place at two rehabilitation stations, both situated in Central Kalimantan (Table 1). In Sumatra data collection took place at two sites of the same station: the quarantine station and at the release site (Table 1).

Depending on available background information the sample collected at the rehabilitation stations was further divided into the following groups: Wild, Station, Human and Unknown. Individuals were assigned to these four groups depending on the estimated age at arrival at a rehabilitation station (based on tooth eruption patterns) and their previous history with humans (Table 2). Table 2 shows that infants are usually caught when very young because then they are still easy to handle and thus most attractive as pets.

Table 2: Categories of subjects and their background histories

Background during early development	N	Age Range (years)	Current Housing	Years in Captivity	Human Exposure	Remark
Wild	5	10-25	Rehabilitation station	0-7	Minimal	Majority of life in natural habitat. Arrived at a rehabilitation center as adolescents or adults, eventually to be translocated to a new natural habitat.
Station	8	5-11	Rehabilitation station	4-10	Mainly human raised	Minimum 80% of life in rehabilitation station. Arrived at station as dependent offspring at the age of 1.5 year or younger.
Human	16	3.5-14	Rehabilitation station	0-9	Minimum 6 months with humans	Arrived at rehabilitation station older than 1.5 years of age. Background history with human contact (minimum 6 months), e.g. pet
Unknown rehab	33	3-17	Rehabilitation station	0.5-14	Unknown before arrival at station	No background information. Arrived at station between 2 and 7 years of age and spent possibly large part of the developmental phase in captivity.
Mother-reared Zoo	31	5-52	Zoo	Whole life	All life within human care	Nursed by own mother within a zoo. All life in captivity with exposure to human caretakers and visitors.
Hand-reared Zoo	10	13-43	Zoo	Whole life	Human hand nursing and all life within human care	Nursed by human caretakers either at the zoo or in human households. All life in captivity with exposure to human caretakers and visitors.

Housing conditions

In the zoos, individuals were housed in mixed-aged groups of conspecifics ranging from four to 12 individuals in standard indoor enclosures during the day, and mostly separated individually or in pairs into sleeping quarters for the night. Most zoos also provide the orangutans with a larger outdoor enclosure. At each zoo, animal keepers are in daily close contact with the orangutans, providing them with food but also with diverse enrichment activities. Zoo visitors were additionally in daily visual contact with the orangutans.

In the rehabilitation stations the housing situations were more heterogeneous (see Table 1). They differed according to the standards and capabilities of each facility and the age, sex and background of the individuals. All orangutans in this study were held in solitary enclosures at the time of the study, except for one station housing 28 individuals socially in groups of 2-6 individuals. In

general contact with humans was reduced to caretakers cleaning and feeding several times a day and veterinary care as needed. Each enclosure had simple enrichment devices, such as ropes, and several times a week the subjects received extra food-related enrichment or leafy branches. In some facilities, small infants lived in a nursery with other orangutan infants and human caretakers serving as replacement mothers. These infants had daily extended contact with their foster-mothers and other human caretakers. Most individuals had access to forest vegetation at some stage during their time at the station.

Human Orientation Index

To capture any psychological variation caused by time in captivity and human-related experiences, we assessed the degree to which each individual reacted toward a novel human. The Human Orientation Index (HOI) contained the following components: reactions and proximity to a human stranger during two conditions. Each subject was tested individually, except for a few cases where the mother was tested with its dependent offspring to avoid inducing stress for both. In the zoos the test took place either in the home enclosure or in the sleeping quarters if individuals were more easily separated there. In the rehabilitation stations, individuals were either transported to single compartments for testing or were directly tested in their home enclosure. The test was performed by a local man, unknown to the orangutans and dressed in black.

The total test lasted for one minute and was composed of two consecutive conditions, each lasting 30 seconds. In the first condition the man approached and positioned himself approximately one meter in front of the enclosure where the subject was located and remained standing with his body oriented laterally (perpendicularly) to the subject. In the second condition the man turned around to face the orangutan and tried to establish eye contact. The whole test was video recorded and during the entire test no other human was present.

Reactions and proximity to the man for the first two seconds of first sight were coded from the videos. For each condition we scored the proximity to the man in the following way: 0= the orangutan positioned itself as far away as possible; 1= the orangutan was more than one meter away from the human; 2= the orangutan was within one meter from the human; and 3= the orangutan placed itself as close to the human as possible.

We also scored the very first behavioral reaction of the orangutan for each condition as follows: 0= a negative reaction, defined as: retreat, stress vocalization, pilo-erection, nervous swinging or turning away from the human; 1= a neutral reaction, defined as resting, moving calmly or play behaviour; 2= a positive reaction, if the orangutan approached the human; and 3= an actively positive reaction, if the orangutan begged (either by using lips or hands), tried in any other active way to contact the human or attempted to trade objects from the enclosure for food.

Furthermore, since the measurements listed above were based upon the first reaction of each condition only, we also scored whether any active contact behaviour occurred during the 30 seconds

of each condition. This was to ensure catching the possible substantial interest in humans, when the surprise had waned.

Thus, in total HOI consisted of all the summed behavioral reactions combined with the proximity to a human stranger, with the eventual score ranging from zero to 14. In our sample, scores ranged from 2 to 14. Furthermore, we also measured the time in seconds a subject spent within one meter of the human stranger throughout the whole test and found that this independent time measurement of proximity was strongly correlated with the HOI-index (Spearman's correlation, two-tailed: r_s=0.600, N=96, P<0.001). Given that an individual can be in close proximity and not move throughout the time of the test, but nevertheless not show any active response behaviour, we used the summarized index of both behavioral reactions and proximity scores, which also generated more resolution to the various responses within our sample, than simply proximity latency data would.

The logistics in one of the rehabilitation stations allowed us to use a sub-sample of 28 individuals to test for social interest in unfamiliar conspecifics. In this sub-sample we measured the time of close proximity to two other unknown orangutans of equal sex, when these were present in a neighboring enclosure to the subject, which allowed us to disentangle social orientation per se to that from interest in humans.

Response to novelty

We performed two separate tests to assess individual variation in novelty response. First, we examined how each subject reacted to novel food. In the zoos, the novel food was blue mash potato served with black olives on top. Zoo orangutans receive a broad diet with many types of human food, but blue items are not common and olives were new to all individuals. In the rehabilitation stations we used purple rice or purple mash potato with dried purple sweet potato pieces. Second, we introduced a novel toy in the form of a wooden board equipped with six differently colored, rotatable tennis balls. For both tasks, we recorded the latency from task begin (when set up was completed and individual was in max. 1 m distance to the apparatus) until first touch, as well as exploration duration of the novel toy. Maximum test duration was two minutes for both tasks, and each subject was tested individually.

Experimental cognitive task – The honey tool-task

In order to evaluate cognitive performance we used a naturalistic task, which required no pre-training trials and could therefore easily be applied to all individuals. The honey tool-task allowed us to assess physical cognition of tool-use at multiple levels from very basic understanding of the apparatus and tools to high innovativeness. The task involved a wooden box measuring 50 cm x 80 cm x 5 cm, whose front was covered by a transparent Plexiglas® or Macrolon® plate (Fig. 1). The upper part of the box contained a straight channel (30 cm x 5 cm) where a wooden stick (40 cm) with its tip dipped in honey had been inserted. Below the straight channel, the box had a L-shaped channel (15 cm

x 10 cm) with its bottom part filled with honey. The honey was visible to the subjects through the glass, but both channels were too long to reach the honey with their fingers. Moreover, the wooden stick could not be used to reach the honey in the L-shaped channel. In addition, below the test apparatus we provided each subject with two more wooden sticks and three pieces of rope. The ropes were too short to reach the end of the straight channel but long enough to retrieve the honey at the bottom of the L-shaped channel.

We measured multiple aspects of the orangutans' responses to the apparatus, which was presented to them in the absence of any humans. To estimate cognitive ability, we measured the following actions: 1) removing the pre-inserted stick from the straight channel; 2) inserting any of the three available sticks into the straight channel during total test time; 3) tool manufacturing, defined as an attempt to modify the provided tools and/ or the use of any other item found by the subjects as a tool for the honey channels; 4) inserting the rope tool into the L-shaped channel. We coded each action separately as yes or no, depending on whether or not a subject performed it (Fig. 1).

Image	Graphic	Task measurement	Definition	Remarks
		Remove stick	Stick provided in the straight channel is taken out	Recognition of the stick in the channel and removal of it
		Insert stick in straight channel	Any of the three sticks are inserted into the straight trap during the 10 minutes test time	Understanding of stick fitting the straight trap
		Tool manufacture/ other tool use	Any tool (stick or rope) is modified or any other material is used as a tool in any of the channels	Innovative attempt to retrieve honey by modifying existing tool or trying out any other solution
		Insert rope in L-curved channel	Any of the three ropes are inserted into the L-shaped channel	Understanding of the properties of rope fitting the L-shape channel

Figure 1. Overview of the design, structure and measurements of cognitive performance. The honey tool-task offered two problems to solve: an upper channel with a stick solution and lower channel with a rope solution.

We also recorded detailed data on any exploration actions during the problem-solving task. These were divided into two main categories: relevant and irrelevant. Relevant exploration concerned the channels, and thus the actual problem to be solved. Any other explorative acts directed toward the test apparatus itself, the board or table was coded as irrelevant exploration. For both categories of exploration, we measured the frequency, the duration, and the variety (see Supplementary Table S3 for definitions).

Experimental procedure

In all tasks (novelty response tests, the HOI test and the honey tool-task), only those individuals participated who could easily be separated without showing any signs of separation-induced stress. Accordingly, sample size across the different tests varied from 94 to 103. In the honey

tool-task each orangutan was tested individually, except for two mothers who were tested with their dependent offspring, in which case the offspring did not participate in the task. All subjects were naïve to this test apparatus and we performed no training trials. All subjects were tested only once. Zoo individuals were tested in their smaller sleeping enclosures where they could be separated from the group. Testing in the rehabilitation stations took place in the home enclosures, since most individuals were housed alone. For the 28 socially housed individuals, additional testing enclosures were available. The individuals were brought to the testing enclosures separately and only stayed there for the time of testing. We therefore incorporated the identity of the rehabilitation station as one factor in our analyses. The problem-solving task lasted a maximum of 10 minutes. Because the individuals' experience with humans was so variable, we conducted the problem-solving task without the presence of an experimenter to avoid possible effects on the subject's participation and attention during cognitive testing (cf. Schubiger et al., 2015). The task was video recorded with one to two SONY HDR-CX200 handy cameras, depending on angle of the cameras. None of the orangutans were food-deprived for the task. In the rehabilitation stations, the honey tool-task was presented to the subjects on a large board right outside of their enclosure, and subjects could easily reach out toward the problem-solving task. In all but one zoo, the apparatus was also presented outside the enclosure. However due to the logistics and narrower mesh size in the zoos, we presented the apparatus closer to the mesh with a slight angle but less accessible to the orangutans compared to the rehabilitation station setting. In one zoo, we presented the honey box within the test enclosure, with orangutans having full access to the apparatus. We therefore incorporated accessibility of the test apparatus as one factor in our analyses.

Data extraction and statistical analyses

All videos were imported into Mangold interact 9.7, in which all detailed behaviors of both cognitive performance measurements as well as exploration acts were coded by SF and LD. We used IBM SPSS Statistics 20 to perform inter-observer reliability tests on every behavioral measure that occurred during the honey-tool task. For the zoo sample, 20% of the videos were coded by both observers and yielded a Cohen's Kappa of 0.842 (N_{events}=1020, P<0.001), which is considered very good. From the rehabilitation sample, 16% of the videos were coded by both observers and yielded a good inter-rater agreement (Cohen's Kappa: 0.721, N_{events}=1020, P<0.001). Also the behavioral responses and the proximity measurements that generated the Human Orientation Index was coded in Mangold interact 9.7 by SF and a trained research assistant AS and reached a good inter-observer reliability value of 0.853 (Cohen's Kappa: $N_{responses}$=52, P<0.001). LD and SF reached an inter-observer reliability value (IOR) of 0.782 (Cohen's Kappa: $N_{responses}$=66, P<0.001) in a sample of over 26.6% of the zoo-videos. LD and AS reached a substantial agreement within the sample of rehabilitation orangutans of 0.701 (Cohen's Kappa: $N_{responses}$= 185, P <0.001).

Further statistical analyses were performed in R version 3.2.3 (Nakagawa & Schielzeth, 2013; R Core Team, 2016) using the 'lme4' (Bates et al., 2015) and 'MUMIn' (Barton, 2016) packages. Individual scores on each of the four measures of cognitive performance (exhibit: Yes/No) were modeled by a binomial Generalized Linear Mixed Model (GLMM). We incorporated each individual's HOI-score, age, sex, species, accessibility of apparatus, and ontogenetic background (rearing and housing condition), along with the measure of cognitive performance (Table 3) as fixed factors, and controlled for repeated observations on each individual within its respective facility by specifying this as a nested random effect. For categorical predictor variables with more than two levels, we manually specified planned contrasts. For accessibility of the test apparatus and the measure of cognitive performance (both ordinal predictor variables), we conducted polynomial trend analyses, while for ontogenetic background we set orthogonal contrasts to compare: 1) wild subjects against all other subjects, 2) subjects from rehabilitation stations against zoo subjects, 3) within rehabilitation stations, subjects from unknown provenance against all other subjects, 4) within rehabilitation stations, human-reared subjects against station-reared subjects, and finally 5) within zoos, hand-reared subjects against mother-reared subjects. To examine each individual's relationship between the HOI scores, novelty response, exploration variables and performance, we used Linear-Mixed-Effect-Models (Fig. 3-5).

Ethical statement

All experiments fully complied with the ethical guidelines of each study facility (zoological garden/ rehabilitation station) and were respectively approved by the research manager and/or head of each facility. We confirm that according to the Swiss Animal Welfare legislation our animal experiments are considered with the severity grade 0 (no harm). The experimental protocols for the rehabilitation stations were approved by the Animal Welfare office of the University of Zurich, the Scientific Advisory Board of the BOS Foundation (Borneo Orangutan Survival), the research managers and head of the stations of Sumatran Orangutan Conservation Program (SOCP) and Orangutan Foundation International (OFI), and the Indonesian Ministry of Research and Technology (RISTEK). Moreover, all zoo experiments were supported by research committee of the British and Irish association for zoos and aquariums (BIAZA).

Results

Cognitive performance

For the honey tool-task, we found large variation in cognitive performance among the 103 orangutans (Fig. 2). Eleven individuals did not solve a single sub-task. The modal and median score on total performance was 1 out of a maximum of 4. The four different cognitive measurements of the

honey tool-task varied significantly in difficulty. In order to examine whether the ability to solve the different sub-tasks was cumulative, we applied a Guttman scale, which showed a reproducibility coefficient of close to one (0.97). This strongly suggests that the ability to solve the more difficult sub-tasks was nested within the performance of the other sub-tasks: 90% of the 103 individuals performing the honey tool-task fitted the applied Guttman scale of the four different sub-tasks (see Methods and Fig. 1 for details). As expected, 'remove stick' was the easiest, 'insert the stick in the straight channel' was next, followed by 'making a tool', whereas 'inserting the rope in the curved channel' was most difficult (Fig. 1, Sub-task) for the orangutans in this study. Due to this variation in difficulty, we treated the four levels of cognitive performance as an ordinal variable in further analyses.

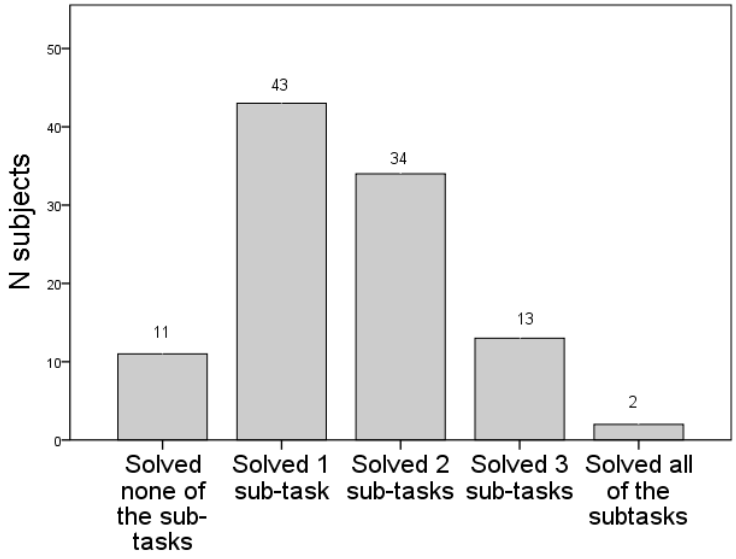

Figure 2: Honey tool-task performance. Frequency of subjects that solved zero to all subtasks.

We next tested whether background and housing conditions, species, sex, and age could explain the variation in cognitive performance on the honey tool-task. Table 3 shows the results of a binomial Generalized Linear Mixed Model (GLMM) of the honey tool-task performance, with the response variable being whether or not a subject solved each sub-task. The GLMM allowed us to control for repeated observations in each facility and on each individual. The results revealed that the human orientation index (HOI) was a good predictor of the ability to solve the task (B±SE= 0.227±0.08, Z=2.699, P=0.007; Table 3), as was the latency to touch unfamiliar food (B±SE= -0.034±0.01, Z=-2.263, P=0.024; Table 3) and a novel object (B±SE= -0.025±0.01, Z=-2.123, P=0.034; Table 3). The less neophobic the individuals, the more likely they were to solve the task. When we removed the novelty responses from the analysis, the HOI remained the main predictor of performance (Table S1, Supplementary material). Because an individual's age and the time it had spent in captivity were strongly correlated, only the factor age was considered for the analysis, but it did not influence task performance. Subtle differences between enclosures, which might affect the ease of access to the apparatus, were controlled for in the analysis, but again did not contribute to

explaining the variation in cognitive performance. Perhaps surprisingly, none of the other possible variables (sex, species [Sumatran or Bornean], and the various background and current housing conditions of the orangutans) predicted performance; they also had no influence on task performance when HOI was excluded from the analyses (Table S2, Supplementary material).

Table 3: Generalized Linear Mixed Model of overall performance in the honey tool-task.
Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task.

	B	***SE***	***Z***	***p value***
(Intercept)	-2.588	1.33	-1.943	0.052
Human Orientation Index	0.227	0.08	2.699	**0.007 ****
Novel food: time until touch	-0.034	0.01	-2.263	**0.024 ***
Novel object: time until touch	-0.025	0.01	-2.123	**0.034***
Novel object: exploration duration	0.003	0.01	0.433	0.665
Age	-0.006	0.03	-0.232	0.817
Sex (male)	0.124	0.51	0.243	0.808
Species (Sumatra)	-0.094	0.59	-0.16	0.873
Background				
Wild vs. Rest	-0.173	0.27	-0.639	0.523
Rehab vs. Zoo	-0.402	0.29	-1.395	0.163
Unknown vs. Rehab.Rest	0.073	0.20	0.367	0.714
Human vs. Station (within rehabilitation station)	-0.479	0.48	-1.008	0.314
Mother vs. Hand (within zoo)	0.365	0.51	0.722	0.470
Accessibility (trend analysis)				
Linear	0.786	0.76	1.04	0.298
Quadratic	0.228	0.89	0.257	0.797
Cubic	-0.189	0.89	-0.213	0.831
Sub-task (trend analysis)				
Linear	-4.969	0.74	-6.737	**<0.001 *****
Quadratic	1.554	0.44	3.559	**<0.001 *****
Cubic	-0.205	0.33	-0.626	0.531

Note: The model is controlling for repeated observations on each facility and individual. The performance in the honey tool-task was binary measured. The Analysis included 88 individuals in 9 different zoos/rehab stations, totaling 352 observations, χ^2= 226.27, P< 0.001, P-values below 0.05 appear in bold.

Exploration behaviour underlying cognitive performance

The orangutans' performance on the tool-use task was best accounted for by exploration variety, which explained 27% of the variation (Fig. 3b and Fig. 4), whereas exploration duration predicted 9% of the variation (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =8.57, $R^2_{LMM(m)}$=0.092, P =0.005, Fig. 3a and Fig. 4). However, the HOI only explained 5% of cognitive performance (χ^2_{ML} =6.21, P<0.05).

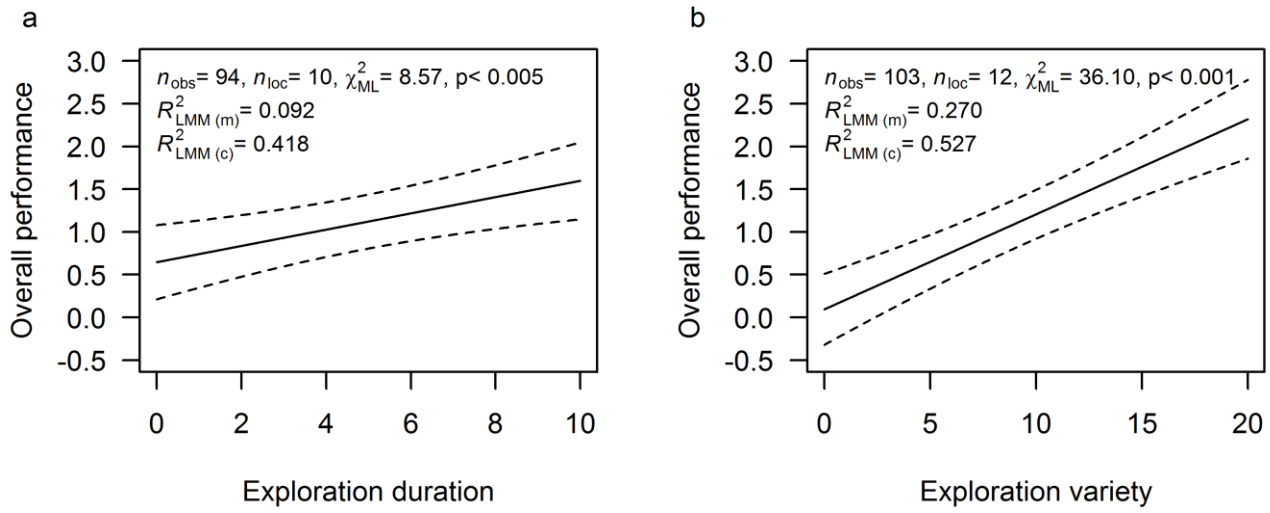

Figure 3. The relationships between exploration behaviour and the overall cognitive performance. (**a**) Overall performance in relation to the exploration duration. Individuals that explored longer were significantly better problem solvers (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =08.57, P =0.005). (**b**) The overall task performance in relation to the total variety of exploration actions (N_{obs}=103, $N_{location}$=12, χ^2_{ML} =36.10, P <0.001).

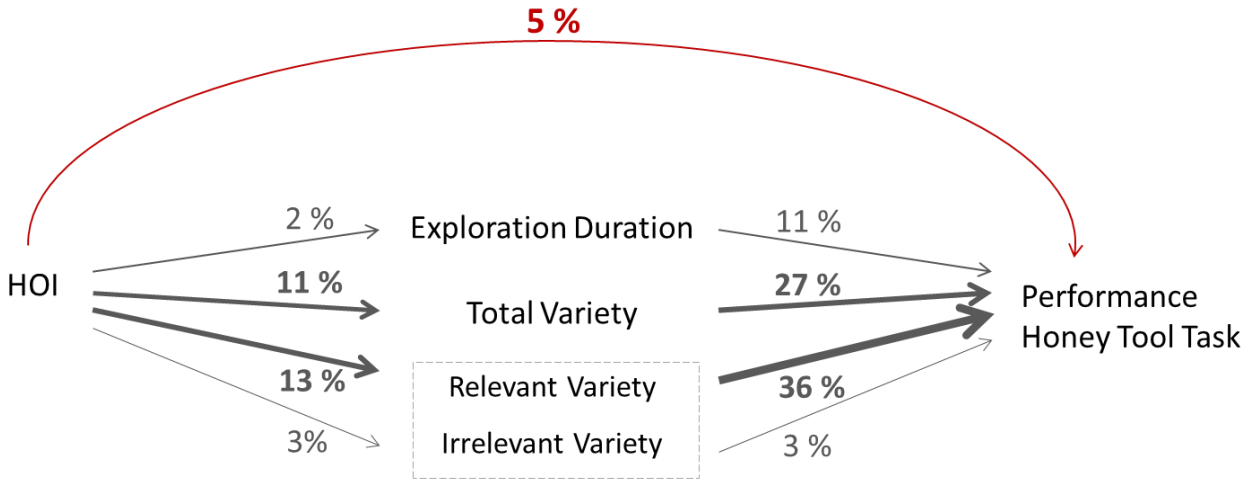

Figure 4. Graphical illustration of the relationship between the human orientation Index (HOI), the cognitive performance and exploration duration and variety, in context to each other. The total variety can be divided into relevant and irrelevant variety. The figure also indicates the percentage of variation estimated by the pseudo R^2 for linear mixed effects margins that is explained by each factor. The thickness of the arrows accentuates the strength of the influence.

The effect of human orientation on exploration

A Linear Mixed-Effects Model (LMM) analysis of the subjects' exploration of the apparatus, which controlled for repeated measurements in each facility, showed that HOI accounted for 11% of the variation of the total exploration variety (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =12.02, $R^2_{LMM(m)}$=0.1113, P <0.001, Fig. 4 and Fig. 5b). In addition, there was a trend showing that individuals with a higher HOI explored the apparatus longer than those with a lower HOI (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =3.53,

$R^2_{LMM(m)}$=0.025, P =0.06, Fig. 5a), although the HOI explained a mere 2% of the variation in exploration duration (Fig. 4). This low proportion is not surprising, because the most successful orangutans, and thus the ones with high HOI values, stopped exploring once they found the solution to the problem and spent their remaining time extracting honey.

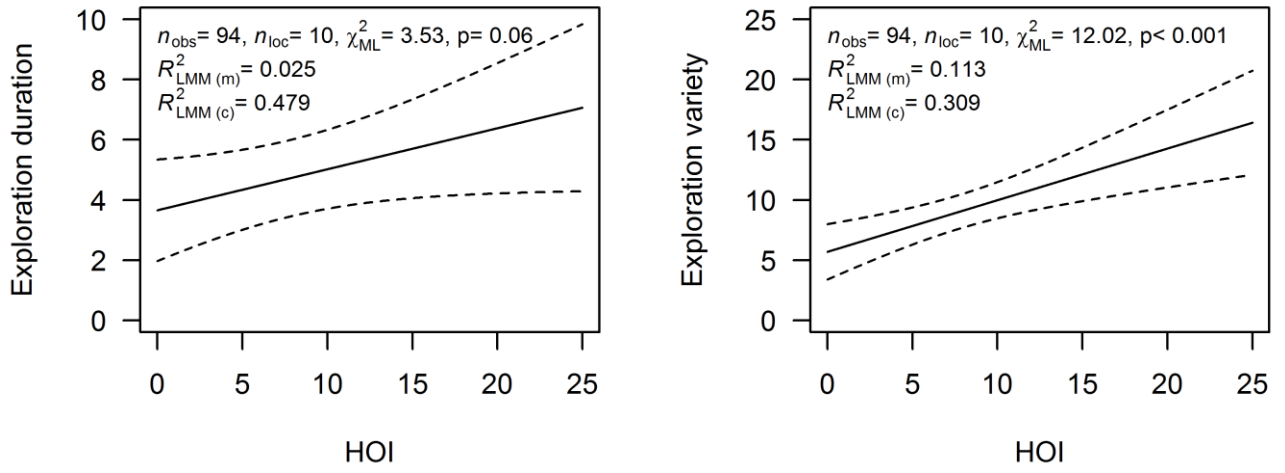

Figure 5. The relationships between the human orientation index (HOI) and exploration behaviour showed significant dependencies in Linear-Mixed-Effect-Models (LMM) that controlled for repeated observations in each facility. (**a**) Exploration duration in relation to HOI-index (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =3.53, $R^2_{LMM(m)}$=0.025, P =0.06). (**b**) Total variety of exploration actions in relation to the HOI (N_{obs}=94, $N_{location}$=10, χ^2_{ML} =12.02, $R^2_{LMM(m)}$=0.1113, P <0.001).

Random exploration of the apparatus per se does not necessarily raise the chances of finding the solution. Individuals who can distinguish between relevant and irrelevant parts of the apparatus should be more successful (Supplementary Table S3). We therefore also investigated the separate effects of exploration variety directed at the relevant or irrelevant areas of the apparatus. We calculated marginal pseudo-R^2 values to estimate the proportion of variation explained by the fixed effects in our model. The HOI explained 13% of the variation of relevant exploration (χ^2_{ML} =13.67, P<0.001, Fig. 4 and Supplementary Table S4), which subsequently accounted for 36% of the variation in cognitive performance. In contrast, HOI explained only 3% of the irrelevant exploration (χ^2_{ML} =2.93, P=0.087, Fig. 4), which accounted for only 3% of performance in the task. The effect of a higher HOI was thus primarily on the amount of exploration and especially on the diversity of exploration on relevant parts of the task, with the latter explaining 36% of cognitive performance. Furthermore, neither housing- nor background/ rearing history had any effect on the exploration of the apparatus (Supplementary Table S4).

Additionally, using a Linear Mixed-Effect Model (LMM), controlling for each subject's housing location, we compared the exploration style of the most successful individuals, the 10 subjects who solved the most difficult problem of 'inserting the rope in the curved channel' ('ropers'), to the other non-successful individuals ('non-ropers'). There was no difference in exploration duration between

ropers and non-ropers. However, the ropers differed significantly from non-ropers in their exploration variety (P= 0.012). Ropers not only showed a greater diversity of explorative actions, but also a far greater diversity of exploration on relevant parts of the apparatus (p< 0.001; note that solving the rope solution is itself not counted as relevant exploration). Moreover, the ropers' HOI was 29.7% (and significantly) higher than that of non-ropers (χ^2_{ML} =4.06, P<0.05).

Evaluating the human orientation index

Given the large effect of the HOI on exploration style, we examined whether the different background categories determined an individual's human orientation index. 'Wild' individuals strongly diverged from any other category in that they took longer or did not respond at all to the novel food and novel object (Supplementary Fig.1) and by showing significantly lower HOI values (Kruskal-Wallis test: N=95, P=0.002, Fig. 6). However, pairwise comparisons of each background category (controlling for age, sex and species as well as repeated observations from each study location and correction of P-values for multiple comparisons using Tukey) revealed no significant differences in HOI between the background categories (Supplementary Table: S5).

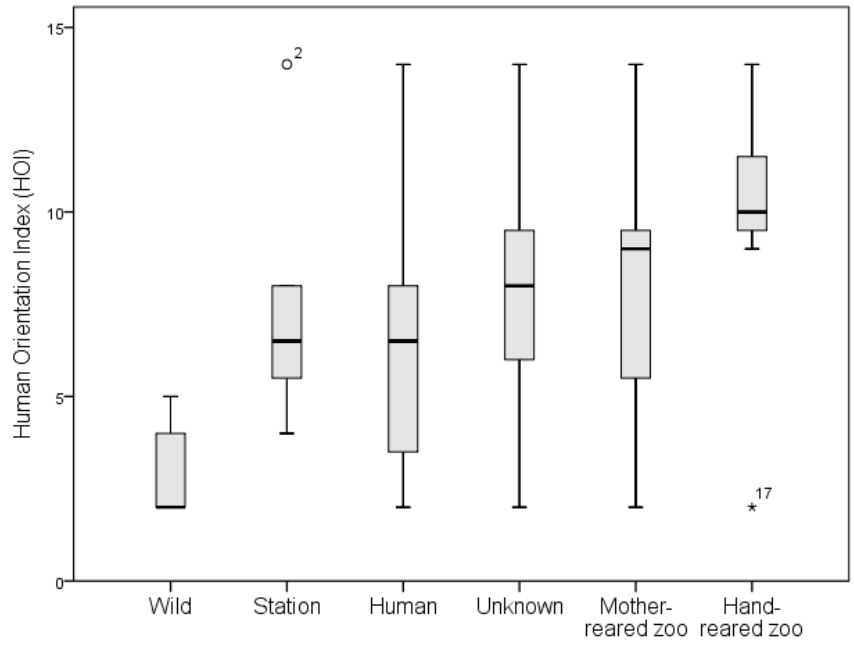

Figure 6: The human orientation index (HOI) in relation to background history. Groups of individuals with different background histories differed slightly in their human orientation.

Table 4: Linear Mixed-Effects model of the Human Orientation Index controlling for repeated observations on each facility.

	Estimate	*SE*	*df*	*t value*	*p value*
(Intercept)	7.155	1.12	58.15	6.401	**<0.001*** **
Novel food					
Latency touch	-0.057	0.06	78.83	-0.977	0.332
Novel Object					
Latency touch	0.001	0.02	81.9	0.457	0.649
Exploration duration	0.006	0.01	81.99	0.584	0.561

Note: N observations = 85, N place = 9, X^2_{ML} *= 3.556, P = 0.314,* P-values below 0.05 appear in bold.

The reaction toward novel humans might also be the result of several other factors, such as a response to any novelty or to social beings (human or orangutan). Therefore, we also examined the links between HOI and the three novelty response experiments (concerning novel food, novel objects and novel conspecifics). Results of a Linear Mixed-Effects Model (LMM) evaluated the relation between the HOI and two other novelty response tasks, the novel-object and the novel-food task. The HOI was not explained by the latency to touch either the novel food (B±SE= -0.057±1.12, *df*= 78.83, t= 6.401, P=0.332; Table 4) or the novel toy (B±SD= 0.008±0.02, *df*= 81.9, t= 0.457, P=0.649; Table 4), whereas the latter two were correlated (Spearman's rho: r =0.314, N=98, P=0.002, 2-tailed). Neither did the exploration duration of the novel toy explain the variation in HOI (B±SE= 0.006±0.01, *df*= 81.99, t= 0.584, P=0.561; Table 4). Thus, the HOI did not simply reflect a positive response to novelty per se. To test whether the HOI represents a general interest in social beings, and thereby a higher social motivation in general or whether it describes the interest in humans specifically, we performed an additional social-interest-task with a subset of individuals of one rehabilitation station (N=28, see Method section). The HOI did not seem to measure a general social interest, since the duration spent in close proximity to a novel human did not correlate with the time spent in close proximity to novel conspecifics (Spearman's rho: r =.198, N=28, P=.312, two-tailed).

Discussion

This study represents one of the largest systematic individual-level comparisons of cognitive tool-using abilities in apes, involving 13 different captive groups in both zoos and rehabilitation stations in which none of the individuals were deprived or enculturated. As expected, the latency to touch novel food or objects, and thus reduced neophobia, was an important independent predictor of task performance (Table 3), as has been found in other studies (Auersperg et al., 2011; Benson-Amram & Holekamp, 2012; Cauchard et al., 2013; Sol, Griffin, & Bartomeus, 2012). However, we also found that variation in problem-solving skills in the honey tool-task was equally predicted by persistent and varied explorative behaviour, which in turn was highly influenced by the orangutans' psychological orientation as assessed with the human orientation index, HOI (Table 3). We suggest the following

biologically most plausible causal cascade, backed up by a series of analyses: Human orientation mainly influenced both the orangutans' motivation to explore and the nature of their exploration, and consequently affected their understanding of the problem-solving task, and thus their success in solving it.

The reaction towards humans could have several dimensions, other than the mere interest in humans, and our results allowed us to characterize the nature of the Human orientation Index (HOI) in more detail. A high HOI does not simply reflect the expectation of food that is provided regularly by humans, because HOI varied extensively and all these orangutans depended on humans for their food. The different background categories also showed higher variability in their HOI than in their novelty response (Fig. 6 and Supplementary Fig. S1). Moreover, if it were mere food expectation, variation in HOI should be associated with caretakers that provide the daily food supply rather than random strangers. Finally, the HOI does not reflect general novelty response or general social interest, as it was not correlated with the approach latency to novel food nor objects (Table 4), nor with interest in novel conspecifics. Therefore the effect was human-specific and increased the motivation to explore, expressed as increased duration and variety of exploration (Fig. 5a and 5b).

The HOI thus captures a fundamental psychological change that is induced by human contact. The different background categories overlapped largely in their HOI (Supplementary Table S5), implying that each individual's specific nature and experience of human contact is more influential than the human exposure time per se. However, our sample included a few wild individuals who had spent their whole immature period in natural habitat and showed very low human orientation compared to most other conspecifics housed in zoos and rehabilitation stations, independent of the time they had spent at the station (Fig. 6). This indicates that the change caused by humans can only happen at an early age, suggesting a sensitive period for social inputs. Since this kind of psychological orientation is absent in nature (Forss et al., 2015), we can ask which natural process is being mimicked or modified by human contact. The answer is remarkably simple: humans replace the role of the mother and other conspecific experts, and the rich variety of artifacts provided by humans enriches their physical environment. In their natural niche, orangutans as well as other primates are prone to attend to their mother and other expert conspecifics and learn necessary skills socially (Humle, Snowdon, & Matsuzawa, 2009; Jaeggi et al., 2010; Lonsdorf, 2006; Schuppli et al., 2016; van de Waal et al., 2010; van de Waal, Borgeaud, & Whiten, 2013). Exploration plays a crucial role in skill acquisition in the wild, but virtually all exploration is socially facilitated, allowing orangutans to overcome intrinsic neophobia (Forss et al., 2015).

Given the identification of human orientation, rather than rearing conditions, as the key determinant of cognitive ability in captive apes, it makes sense to revisit the role of deprivation and enculturation. Because deprivation involves the complete loss of any role models, whereas enculturation involves the presence of far richer social inputs by more actively engaged role models than under normal conditions, one could argue that the degree of human orientation may largely explain the whole spectrum of cognitive performance among great apes. This perspective also explains

why enculturated apes outperform others not just in socio-cognitive skills, but also in physical cognitive skills (Bard et al., 2014; Rumbaugh & Washburn, 2003).

The social triggering of the engagement with artifacts is highly influential in human child development (Bard & Leavens, 2009; Tomasello, 1999). Studies within the field of comparative psychology have documented nonhuman primates' tendency to attend to humans (Call & Tomasello, 1996; Hirata, Morimura, & Houki, 2009) and acknowledged the improvement in learning cognitive tasks due to human contact in captive settings (Harlow, 1949; Rumbaugh & Pate, 2014). Systematic species comparisons of primates' attention structure toward humans are rare. Nonetheless, in 1916, Yerkes (Yerkes, 1916) already suggested that the qualitatively better cognitive performance of an orangutan compared to monkeys was due to the ape's social attention to human actions. Our results thus support previous suggestions (Byrne & Russon, 1998; Russon & Galdikas, 1993; Shumaker, Walkup, & Beck, 2011) that early exposure to humans and human artifacts presents a broader range of opportunities for exploration resulting in increased innovativeness in captive apes. Over time, the accumulating experience resulting from attention to humans leads to improved problem-solving ability, provided the exposure to humans is early in life. In conclusion, human orientation at least partly explains the phenomenon that captive primates that are exposed to both conspecific and human role models experience increased opportunities for socially induced exploration and learning (cf. Bering, 2004).

Our detailed analyses revealed that the HOI influenced an individual's duration and especially its variety of exploration (Fig. 5a and 5b), which subsequently explained cognitive performance (Fig. 3a and 3b, Fig. 4). Previous studies on hyenas (Benson-Amram & Holekamp, 2012) and birds (Griffin & Guez, 2014) have also reported that the diversity of exploration actions influences innovativeness and problem-solving skills. However, in our study, individuals with a strong human orientation were more successful in the task, not only through their exploration diversity, but also by focusing on the relevant parts of the apparatus (Fig. 4), implying that they were better at recognizing the actual challenge presented in the honey tool-task. Importantly, these parts were relevant not because they directly led to the solution, but rather because exploration of these parts improved the animals' understanding of the physical properties of the problem. For example, individuals that traced the honey channel from the outside of the glass obviously understood that there is honey inside, but were at that time not searching at the correct part of the apparatus, the channel entrance. Similarly, individuals poking with their finger into the curved channel may have gathered information on its length. Exploration can therefore be viewed as latent learning: it allows an animal to gather knowledge of the texture, the material, and the problem itself. Over time, then, individuals with a high HOI will gain more experience, which contributes to their focus on relevant aspects of the problem and hence problem-solving success.

The effects of the HOI on problem-solving success may have been so strong that they masked the effects of other factors. Thus, we found no differences between the two orangutan species (*P. abelii*

and *P. pygmaeus*), even though these were found when orangutans with very similar backgrounds (all mother-reared zoo individuals) were compared on a range of cognitive tasks (Forss et al., 2016).

This study documented strong effects of human orientation on problem-solving abilities, through its effects on response to novelty, motivation to explore, exploration persistence and ultimately experience. This finding suggests that it is just as impossible to design culture-free cognitive tests for primates as it is for humans. In this sense, tests of primate cognition are inevitably deeply anthropomorphic. However, once we have controlled for the subjects' human-related histories and given that problem-solving ability is about dealing with unknown, novel problems the variation captured in these tests nonetheless reflects variation in intrinsic cognitive abilities and should be comparable within and across species. Therefore, we suggest the HOI may be a useful tool in standardizing comparisons across primates, especially studies concerning ape subjects with various background and human-related experiences. In future work, we will further disentangle the exact nature and causes of the HOI and address additional problem-solving domains.

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Chapter 2

Curiosity boosts orang-utan problem-solving ability

Curiosity boosts orangutan problem-solving ability

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Investigating the mechanisms underlying individual variation in cognitive performance is a crucial step towards understanding the structure and evolution of cognition. In this study, we investigated phenotypic plasticity of 61 Bornean, *Pongo pygmaeus*, and Sumatran, *Pongo abelii*, orang-utans to gain insight into how rearing history shapes problem-solving approaches. We first examined the determinants of an individual's response-and-exploration style, which we assessed using five independent novelty response and exploration tasks. Our findings revealed that both previous care by humans and social housing with conspecifics elicited a curious response-and-exploration style (characterized by a positive response to novelty and a high motivation to explore). Second, we investigated how the response-and-exploration style and previous experiences affected an individual's problem-solving performance in a variety of tasks aimed at assessing physical cognition, including reversal learning, inhibitory control, causal reasoning and tool use. We found curiosity to be the sole predictor of problem-solving performance. However, curiosity is strikingly rare in wild orang-utans, being mainly induced by contact with humans and living in a safe and stimulating physical and social environment. We therefore suggest that curiosity in orang-utans is an artefact of captivity, a potential only expressed under special conditions. The origin of curiosity in our own lineage may have been an important contributor to the rapid rise in the complexity of our ancestors' material culture.

Introduction

Individuals of a given species tend to vary in cognitive performance, as expressed for instance in problem-solving ability (Griffin & Guez, 2014; Herrmann & Call, 2012; Neisser et al., 1996; Nisbett et al., 2012; Thornton & Lukas, 2012). Numerous experiments have shown that adult cognitive performance in animals is affected by environmental conditions during early development, be they enriched physical environments (Cooper & Zubek, 1958), enhanced nutrition (Arnold, Ramsay, Donaldson, & Adam, 2007), enculturation (Call & Tomasello, 1996; Tomasello & Call, 2004) or extreme social deprivation (Brent, Bloomsmith, & Fisher, 1995; Mason, 1968; Schrijver, Pallier, Brown, & Würbel, 2004; van Schaik & Burkart, 2011). However, the actual psychological mechanisms, such as exploration and social learning plus their feedbacks, through which these developmental effects are produced, are still only partially documented. Nevertheless, identifying them is vital for understanding the development of cognition as well as its evolution (Rowe & Healy, 2014; Thornton & Lukas, 2012).

Among humans, curiosity is often seen as an important contributor to creativity (Day & Langevin, 1969), decision making (Hirschman, 1980) and innovation (Carr, Kendal, & Flynn, 2016). Curiosity is defined as a motivation towards the acquisition of novel information (novelty seeking) and thus an attraction towards learning and experiencing something new (Berlyne, 1950, 1960; Collins, Litman, & Spielberger, 2004; Litman, 2005; Loewenstein, 1994). Accordingly, curiosity is reflected in approaching and exploring novel stimuli (Berlyne, 1960; Loewenstein, 1994), which makes it a potentially important ingredient of innovation and problem solving (Kummer & Goodall, 1985), for example through trial and error. Therefore, one major factor for the evolution of intelligence and culture in humans may be our curiosity, which makes us seek and explore novelty.

Curiously, although studies of animal problem solving and innovation consider a variety of mechanisms (Griffin & Guez, 2014; Tebbich, Griffin, Peschl, & Sterelny, 2016; van Schaik et al., 2016), curiosity is rarely mentioned (see Kaufman & Kaufman, 2015; but see Benson-Amram et al. 2013). This rarity may reflect the fact that in their natural environment individuals must be vigilant for predators and rivals and are preoccupied with planning their daily routines (Greenberg, 2003), and thus cannot afford to respond to novelty and engage in time-intensive exploration (with rare exceptions: e.g. Diamond & Bond, 1999). In wild orang-utans, *Pongo* spp., for instance, exploration overwhelmingly occurs when initiated by the observation of trusted experts (Schuppli et al., 2016; van Schaik et al., 2016). This preference for social learning may reflect the risks attached to exploration, such as injury or poisoning, especially when the items are novel, which they inevitably are for infants. Interestingly, whereas wild orang-utans avoid

novelty, orang-utans in zoos seek novel stimuli (Damerius et al., 2017; Forss, Schuppli, Haiden, Zweifel, & Van Schaik, 2015). The captivity effect (reviewed in Haslam, 2013) partly reflects this difference in novelty response.

This unexpected juxtaposition of strong conservatism and seeming curiosity within the same species in different conditions raises the question of how curiosity is elicited. One possibility is that captivity offers a safe and stable environment, which includes a reduced need to find and process food and thus increased free time, reduced need to be vigilant for predators and plan travel routes and thus reduced cognitive load, and permanent gregariousness and thus more frequent opportunities for social learning. These circumstances allow individuals to approach and explore novel items and situations (Forss et al., 2015; van Schaik et al., 2016), which, over time, results in larger skill repertoires (Haslam, 2013). In addition, the ability to attend to humans and their actions may increase an individual's knowledge of affordances or stimulate different cognitive processes (Fredman & Whiten, 2008) and might therefore indirectly stimulate innovation propensity. This idea is supported by recent findings in orang-utans (Damerius et al., 2017) showing that human contact during ontogeny led to changes in the orang-utan's attention structure that positively affected individual's problem-solving success. Thus, it appears that captivity may unleash curiosity in animals that are decidedly uncurious in the wild.

The goal of the present study was to examine how important curiosity was in problem solving by linking individual variation in problem-solving ability to response-and-exploration styles in a large sample of orang-utans from widely varying backgrounds. In this work, we wanted to complement earlier studies that suggested enhanced curiosity in captivity (Benson-Amram, Weldele, & Holekamp, 2013; Damerius et al., 2017; Forss et al., 2015) in three ways. First, previous studies generally focused on the effect of single variables, either the absence of neophobia or aspects of exploration, on problem solving. However, response to novelty and exploration styles may have distinct underlying psychological substrates (Carr et al., 2016; Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann, 2014). We therefore used a multidimensional approach that includes a variety of measures to disentangle the various possible contributing factors. Second, most results relating curiosity to cognitive problem solving were only based on a single task (Benson-Amram et al., 2013; Damerius et al., 2017). However, given possible variability in performance across different tasks (Griffin & Guez, 2014; Herrmann & Call, 2012; Herrmann, Hare, Call, & Tomasello, 2010), one ideally includes an array of problem-solving tasks that may recruit different cognitive abilities. Third, previous studies tended to have small sample sizes and therefore lacked explanatory power and resolution (Cole, Cram, & Quinn, 2011; Thornton & Lukas, 2012). We therefore tested a sample of 61 Bornean, *Pongo pygmaeus wurmbii*, and Sumatran, *Pongo abelii*, orang-utans.

The present study was structured as follows. First, we combined a measure of the orang-utans' attentiveness towards humans with various independent assays of response to novelty and exploration to gain broader insight into the nature and causes of interest in the social and physical environment. Second, because we included individuals housed in four Indonesian rehabilitation stations with various rearing histories, we could investigate the effects of individual experiences on their response-and-exploration styles. Third, we examined whether individual rearing histories or the response-and-exploration style most strongly affected their physical problem-solving abilities. We did so using a battery of tasks encompassing different domains of cognition: associative and reversal learning, flexibility, inhibitory control, causal reasoning and tool use.

Methods

Study Subjects and Species

We studied 61 orang-utans housed at rehabilitation stations in the Republic of Indonesia: 45 individuals in Central Kalimantan, Borneo and 16 near Medan and Jambi, both on Sumatra (Supplementary Table S1). Most were born in the wild but captured as young infants and kept as pets before being confiscated by the police and brought to the rehabilitation stations. Other adolescent or adult orang-utans came directly from the wild after being rescued when their habitat was lost to deforestation and conversion to plantations. We classified individuals into four different background groups (Wild, Station and Human, as well as Unknown; see Table 1), based on their age at arrival at the station and previous exposure to humans. Importantly, individuals in the Human category had lived a minimum of 6 months as pets. The ages of the subjects ranged from 3.5 to ca. 25 years. In the wild, age at weaning is around 6–7 years and age at first reproduction, for females, around 13–15 (Wich et al., 2004).

Table 1: Categories of subjects and their background histories

Background	Human exposure	Age (years)	Years in captivity	Qualitative description	*N*
Wild	Minimal	10-25	0-7	Entered the rehabilitation station directly from their natural habitat, often as adolescents or adults	5
Station	Mainly station-raised	5-11	4-10	Arrived at station as dependent offspring at the age of 1.5 years or younger. Hence, spent minimally 80% of life in rehabilitation station	8
Human	Minimum 6 months as pets with humans	3.5-14	0-9	Older than 1.5 years upon arrival. Background history includes a minimum of 6 months of human contact as pet	16
Unknown	Unknown before arrival at station	3-17	0.5-14	No background information, but not reported to be wild. Arrived at station at ages 2-7 and therefore spent a large part of the developmental phase in captivity	32

Study Facilities and Housing

Data collection occurred between June 2012 and June 2014 by L.D., Zaida Kosonen (Z.K.) and a trained assistant (Andreas Wendl) in four facilities of three organizations across Sumatra and Central Kalimantan, Borneo.

Eleven Sumatran orang-utans (four females, seven males) were studied at a quarantine station in Batu M'Belin (QBM), Medan, North Sumatra, which is run by the Sumatran Orangutan Conservation Program (SOCP). Their ages ranged from 5 to 10 years and we tested them in their home enclosures, as they were housed alone. We also studied one solitarily subject (male) and four socially housed subjects (females) aged between 3 and 6 years at Danau Alo, Bukit Tigapuluh, Jambi, Sumatra (SOCP).

Of the Bornean orang-utans in our study, 28 (11 females and 17 males) were at the Orangutan Care Center and Quarantine (OCCQ) in Pasir Panjang, Central Kalimantan. This facility is managed by the Orangutan Foundation International (OFI). The subjects' ages ranged from 8 to 14.5 years. Testing occurred in external test cages, since all individuals were socially housed in same-sex peer groups of two to six individuals. We also studied 17 subjects (seven females, 10 males) at Nyaru Menteng Rescue Center, Palangka Raya, Central Kalimantan. This rehabilitation station is managed by the Bornean Orangutan Survival Foundation (BOSF). The subjects were 6–17 years old and were tested in their home enclosures.

To prepare orang-utans for release, contact with humans at all stations was limited, apart from routine check-ups by veterinarians and cage cleaning and feeding by caretakers

several times a day. In the Bornean facilities, individuals that arrived as dependent offspring were placed in the stations' nursery, where human caretakers served as temporary surrogate mothers. All infants received close physical care and supervision. All enclosures contained simple enrichment devices, such as tyres, ropes and platforms. All stations offered food-related enrichment several times a week and depending on the age and stage of rehabilitation most individuals went for regular forest walks.

Assessment of the Response-and-Exploration Style

The orang-utans' response-and-exploration style was assessed using five independent tasks, in which we recorded their behaviour towards (1) a novel human, (2) a novel object, (3) a novel food item, (4) a familiar food item and (5) a snake model (Fig. 1). This resulted in 13 different measurements that contributed to assessing the response-and-exploration style (Table 2).

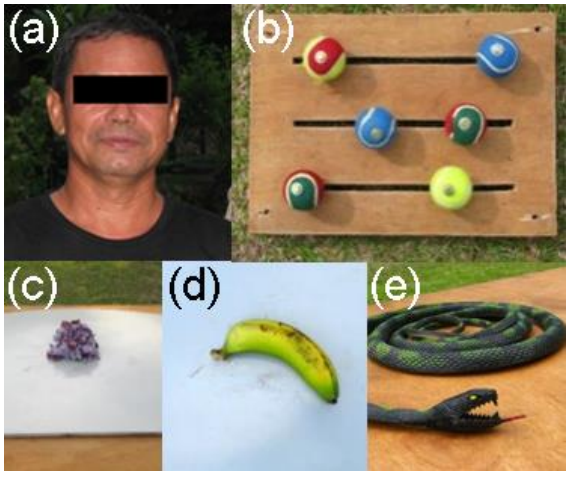

Figure 1: Pictures of the response and exploration tasks: (a) novel human, (b) novel object, (c) novel food, (d) familiar food, (e) plastic snake.

The novel-human task is an extended version of the human orientation index (HOI), which captures an individual's attentiveness towards humans (Damerius et al., 2017). The reactions and proximity to a male human stranger during four conditions were measured (Table 2). Detailed descriptions on how to calculate the HOI for each condition are given in the Supplementary Material. The reaction towards the snake predator model was rated from -2 (negative: retreat, signs of stress such as vocalizing), -1 (avoidance), 0 (neutral reaction) and +1 (approach or trying to scare away the snake model) to +2 (positive: approach, making effort to directly contact the predator, e.g. reaching for the model).

Each task was presented from the outside of the enclosure and lasted 2 min. The order was randomized and the tasks performed on different days, with a maximum of two tasks per day.

Table 2: Detailed description of the response and exploration tasks

Type of experiment	Experiment	Resources	Measures	Task procedure
Novelty response	Novel human (HOI)	Local male human (Fig. 1a)	We measured the duration an individual spent close to the novel human (≤1 m proximity to enclosure front). Further, the first reaction's intensity and position of the orang-utan per condition were recorded, allowing us to calculate the HOI. For more details, see the Supplementary Material and Damerius et al. (2017)	The task duration was 2 min, with four conditions (each 30 s). (1) The man positioned himself 1.5 m in front of enclosure. His body was oriented perpendicularly to the subject. (2) The man turned to face subject and tried to establish eye contact. (3) The man held preferred food (peanuts) out of the individual's reach. (4) The man offered and presented the food to the orang-utan, without actually giving it
Exploration and novelty response	Novel object	Wooden board with six rotatable, coloured tennis balls (Fig. 1b)	We measured the duration of gentle exploration, the duration of rough exploration, the variety of exploration actions, the percentage of rough exploration actions, the latency of an individual's first approach to within 1 m, and the latency until the individual touched the apparatus (after approach to 1 m)	The novel object task was presented on the presentation table for 2 min
Novelty response	Novel food	Purple rice or purple potato mash (coloured with food dye) with pieces of olive (Fig. 1c)	We measured the latency until the orang-utan touched the novel food, and the latency from touching until eating the novel food	The novel food task was presented on the presentation table for 2 min
Novelty response	Familiar food	Familiar food item, selection depended on availability at the station (Fig. 1d)	We measured the latency until the orang-utan touched the familiar food, and the latency from touching until eating the familiar food	The familiar food task was presented on the presentation table for 2 min

Predator model	Snake	Plastic snake, moved by pulling an attached fishing line (Fig. 1e)	We measured the individual's position and intensity of its reaction to the predator model, allowing us to calculate a snake reaction index	The task duration was 2 min with four conditions, each lasting 30 s. (1) The snake rested 1 m in front of the enclosure on the presentation table. (2) The line was pulled, moving the snake. (3) The snake was not pulled and did not move. (4) The line was pulled to move the snake

HOI: human orientation index.

Physical cognitive test battery and procedure

To test different domains of cognitive performance, we exposed the 61 individuals to five different experimental tasks, which yielded six tests: Detour Reaching, Reversal Learning, Box Task, Honey Tool Task (two tests on same task) and Tube Trap Task. The experiments required no pretraining and, except for tasks requiring multiple sessions, were presented just once, in random order, on consecutive days and on a specially designed table (Supplementary Fig. S1). We used the same experimental tasks and procedures for each facility, but customized the size and fixation of the presentation table. Subjects were able to interact freely with the apparatus right outside their enclosure by reaching through the bars. So as not to bias the tests in favour of orang-utans familiar with humans, no human was present during testing, and the apparatuses were set up by a familiar caretaker whenever possible.

The following experiments were part of the cognitive test battery.

(1) Detour Reaching

The Detour Reaching experiment is a classical inhibitory control task and serves as a key predictive measure of problem-solving skills in human and nonhuman animals (Amici, Barney, Johnson, Call, & Aureli, 2012; Carlson & Moses, 2001; Vlamings, Hare, & Call, 2010). A transparent Makrolon box that had two openings at the front, one small hole on the right and a large one on the left, was presented for 5 min (Supplementary Fig. S2). A preferred fruit/enrichment object that was too big to fit through the small hole was placed directly behind the small hole in the right half of the box. The subject could only get the reward by reaching through the large opening and making the detour, and thus had to inhibit the urge to select the putative direct solution. The criterion for success was retrieving the reward.

(2) Reversal Learning.

In a widely used paradigm (reviewed in Izquierdo, Brigman, Radke, Rudebeck, & Holmes, 2016), subjects at first learn that certain items (location, colour) are linked to a reward whereas the other items are not. Once the individual has learned the causal link, the rewarding of the

items is reversed. In the current study, the subjects were presented with a board with square black and round white doors on either side of it (Supplementary Fig. S3). The doors could be swung open by turning them to the right or to the left and gave way to a space filled with a peanut. A randomly determined side was baited. Therefore, when the subject opened a baited door, it was rewarded. The task for the subject was to learn the association between the hidden food and the respective location, which was enhanced by the different colours and shapes of the doors. As soon as the location of food was accurately associated, the location of the reward was switched. If at least five of the first six opened doors were of the correct location for two consecutive trials, the criterion for learning/reversal learning was fulfilled. The board was presented for 4 min per trial, with three to four consecutive trials per day (in total up to 16 min/day). The reversal learning board was presented to the individual for a maximum of 4 days. The criterion for success was the individual's ability to learn the new association (reversal learning).

(3) Box Task

This experiment allowed us to assess flexibility. It consisted of two consecutive presentations of five identical wooden boxes, each with a lid and a sliding door (Supplementary Fig. S4). In the learning phase (4 min), the lid of all five boxes could only be opened by flipping it. Individuals learned that they could flip open the box to receive the reward, a peanut. When four of five boxes were flipped open the learning criterion was fulfilled and the second condition was presented, which constituted the actual test for flexibility (7 min). The lids were locked, and the previously learned solution had therefore become nonfunctional. Now, the sliding doors were unlocked and the boxes baited again out of view of the subject. The criterion for success was successfully passing the learning phase and opening five boxes in the flexibility phase.

(4) Honey Tool Task

This task assessed physical cognition, specifically the abilities to use tools and engage in causal reasoning to select the correct tool for two test locations. The subject was presented for 10 min with the opportunity to fish honey out of two channels. The apparatus consisted of a wooden box with two embedded tubes (a straight channel and a curved L-shaped channel) behind a Makrolon plate to ensure the honey in the tubes was visible (Supplementary Fig. S5). The subject was offered two different tools: three long sticks (40 cm), one of which was already inserted in the straight channel, and three ropes (20 cm). The sticks could be used to extract honey from the straight channel, but not from the curved channel. The rope was too short for the straight channel, but fitted the curved L-shaped channel. Both channels were too long for an

orang-utan's finger to reach the honey. The criteria for successful performance were (1) inserting the stick in the straight channel and (2) inserting the rope in the L-shaped channel.

(5) Tube Trap Task

Causal reasoning and learning ability were needed to successfully solve this task. It consisted of six horizontally placed tubes with open tube ends but an opaque trap left or right from the centre. The tubes were fixed on the vertical board (Supplementary Fig. S6). The front sides were transparent and contained a slit wide enough for an orang-utan finger to slide food inside the tube, allowing the subjects to slide the food reward to the left or right tube opening. However, if the food was moved in the direction of the trap, the food fell into it and was lost (Supplementary Fig. S6a). The task for the subjects was to learn to slide the food in the correct direction. The board with the tubes was presented to the subjects on three consecutive trials of 4 min each. In total the subjects were given the opportunity to explore 18 randomly distributed tubes to learn to avoid the trap. The criterion for success was solving a minimum of 12 of 18 (67%) tubes.

Data extraction and statistical analyses

All experiments were videotaped with two Sony camcorders (HDR-CX200 high definition handycam 5.3 MP), yielding ca. 250 h of video footage, which we imported into Interact, version 9.7.5.0 (Mangold International GmbH, Arnstorf, Germany), for coding of exploration, cognitive performance, latencies and durations. L.D. coded most experiments, but Z.K. coded the Box Task in the stations OCCQ and SOCP. The tasks for the measurements of the response-and-exploration style were partly coded by a trained assistant (Anna Schöpfer). We performed interobserver reliability tests for these tests. All reached substantial agreement. L.D. and Z.K. doubly coded 35% of the Box Tasks videos (Cohen's Kappa= 0.79, $P<0.001$), L.D. and A.S. overlapped for 21% of the coded videos of the response and exploration tasks (Cohen's Kappa= 0.70, $P<0.001$).

All statistical analyses were performed in R version 2.1 and 3.3.1 (R Core Team, 2016) using the 'psych' (Revelle, 2017), 'lme4' (Bates, Maechler, Bolker, & Walker, 2014) and 'lmerTest' (Kuznetsova, Brockhoff & Christensen 2016) packages.

First, we applied an unrotated principal component analysis (PCA) on the 13 measures of the response-and-exploration style (Table 2) using the 'psych' package. We chose not to rotate the components, because we were interested in capturing as much of the total variance as possible in the raw data. With the fa.parallel function from the 'psych' package we tested our observed data against 1000 randomly simulated data sets with equal n and k. Randomly simulated data sets were generated by resampling and generating random normal data. This

analysis showed that the first three components with an eigenvalue of 4.19, 1.78 and 1.62 exceeded the 95th percentile of the eigenvalues obtained from randomly generated data (Supplementary Fig. S7), and are thus significant at the 95% level. Therefore, we repeated the PCA with only three components. We used the first principal component ('curiosity') as response variable in a univariate linear mixed-effects models (LMM) with sex, age, age of arrival at the station and background as fixed effects, to assess the influences on the response-and-exploration style. The LMMs controlled for nonindependence within the different stations by using rehabilitation station as a random effect. Marginal R^2 values (Nakagawa & Schielzeth, 2013) were computed to test the strength of influence of age of arrival at the station, background and number of cage partners on the first component (Fig. 2).

We used a generalized linear mixed-effects model (GLMM) with a binomial link function to model the six individual scores (each coded as pass/fail) on the five tasks. The model controlled for the repeated observations of each rehabilitation station and individual as a nested random effect, and incorporated each individual's sex, age at testing, age of arrival at the station (to control for possible sensitive periods), number of cage partners during the test period, health, background, facility, the response-and-exploration style principal components and the different tasks of cognitive performance as fixed factors. The contrasts for the categorical predictor variables Facilities, Background and Task were specified a priori to compare (1) Sumatran to Bornean facilities and further within Bornean facilities; (2) wild individuals versus all others, individuals with 'Unknown' background versus the 'Station' and 'Human' backgrounds, and 'Station' versus 'Human' backgrounds; (3) wooden tasks versus tasks containing artificial material, e.g. transparent plastic, and Detour Reaching Task (completely made out of transparent plastic) compared to all other tasks to identify whether the type of material used had an influence on the problem-solving performance. The other task contrasts were specified to control for independence between the tasks: the Box Task versus the Reversal Learning Task both presented on the presentation table, the Tube Task versus both Honey Tool Tasks presented with the vertical board, and, lastly, between the Honey Tool Tasks.

Ethical note

All experiments fully complied with the ethical guidelines of each study facility, the Indonesian Ministry of Research and Technology (RISTEK) and were approved by the Animal Welfare officer of the University of Zurich. We confirm that according to the Swiss Animal Welfare legislation our animal experiments carry the severity grade 0 (no harm).

Results

Response-and-Exploration Style

The responses towards novel food, a novel object, a novel human, a predator, familiar food and the exploration of the novel object, were measured in various ways to capture each individual's personal response-and-exploration style. An unrotated principal component analysis (PCA) on the 13 task measures yielded three components (Table 3). The Kaiser–Mayer–Oklin measure verified the sampling adequacy for the PCA (KMO = 0.71), which is 'good' according to Field (2013). Table 3 shows the factor loadings of each variable on the different principal components.

Table 3: Principal component analysis of the response-and-exploration style

Variable	Factor loadings			
	Curiosity (PC 1)	**(PC 2)**	**(PC 3)**	
% Variance	32.26	13.73	12.48	h^2
Eigenvalues	4.19	1.78	1.62	
Latency to touch novel food	**-0.80**	0.23	-0.20	0.74
Latency from touching to eating novel food	**-0.80**	0.24	-0.22	0.75
Human orientation index (HOI)	**0.70**	0.06	-0.28	0.57
Latency to touch novel object	**-0.69**	0.34	-0.01	0.59
HOI duration close to human	**0.67**	0.06	-0.28	0.53
Duration of gentle exploration of novel object	**0.59**	-0.21	0.16	0.42
Variety of exploration of novel object	**0.59**	-0.22	**-0.42**	0.58
Latency to touch familiar food	**-0.58**	**-0.56**	**-0.44**	0.84
Latency to approach novel object	-0.19	**-0.73**	-0.12	0.58
Latency from touching to eating familiar food	**-0.53**	**-0.53**	-0.33	0.67
Snake reaction index (SRI)	0.11	**-0.50**	**0.41**	0.43
% Rough exploration of novel object	0.35	0.17	**-0.71**	0.66
Duration of rough exploration of novel object	0.12	0.25	**-0.43**	0.26

N = 61, rotation = none. Factor loadings greater than or equal to |0.4| appear in bold.

The first component (PC 1) gathered characteristics that represent a positive novelty response towards novel humans, objects and food, along with a high duration and variety of exploratory actions. It accounted for almost a third of the total variance in our sample. Therefore, PC 1 can be characterized as 'curiosity': individuals with a high score were actively seeking the unfamiliar, interested in their environment and exploration-prone. However, orang-utans scoring high on PC 1 were not obvious risk-takers, given their low score on rough exploration (such as hitting the apparatus) and neutral reactions towards the snake. High-scoring individuals in PC 2 had short latencies to touch and consume the familiar food, but not

the novel food. They approached unfamiliar objects up to 1 m, but did not necessarily touch the object faster, or explore it. They also expressed cautiousness towards the snake model. Individuals scoring high on PC 3 were especially unlikely to explore the novel object in a rough manner. Because the components were not rotated, PC 2 and PC 3 did not have unambiguous interpretations and low eigenvalues, so we do not consider them further.

What shapes an individual's curiosity?

A test of the effects on PC 1 of the response-and-exploration style clearly showed that 'wild' individuals were significantly (and very much) less curious (Table 4, Supplementary Fig. S8). We could not detect a significant effect of sex, age at testing or number of cage partners during the period of study. However, individuals that were older at the time of arrival at the station (and thus on average had been in contact with humans longer) tended to be more curious.

Table 4: Parameter estimates and associated standard errors, obtained from a linear mixed-effects model of PC 1 'curiosity' over all 61 individuals

	Estimate	**SE**	***df***	***t***	***P***
Intercept	-0.516	0.536	7.32	-0.963	0.366
Sex (male)	0.094	0.192	52.67	0.489	0.627
Age	-0.059	0.041	33.02	-1.438	0.160
Age on arrival at station	0.099	0.055	47.19	1.800	0.078
Current no. of. cage partners	0.154	0.094	40.60	1.643	0.108
Background					
Wild vs Others (Station/Human/Unknown)	-0.785	0.124	51.19	-6.360	**<0.001**
Station/Human vs Unknown	-0.093	0.070	51.26	-1.333	0.189
Station vs Human	-0.045	0.155	51.38	-0.293	0.771

The model controls for repeated observations on each rehabilitation station (random effect). $N_{observations}$ = 61, $N_{stations}$ = 3, χ^2= 53.768, P< 0.001. Significant P value is in bold.

Because individuals classified as 'wild' had recently arrived at the station and were estimated to be much older on average when first captured than the others (mean ± SE: 15 ± 6.5 years), the strong effect of being wild might have masked any other possible effects on curiosity. We therefore repeated the analysis with the 'wild' individuals removed. The analysis of the remaining 56 individuals showed that the age of an individual when arriving at the station and the number of cage partners had significantly positive effects on curiosity (Table 5). Because individuals are predominantly captured at a young age, this result could suggest that time spent with humans strongly increases curiosity (Fig. 3a). We confirmed this assumption by repeating the analysis with the subsample of individuals (N=16), for whom we knew with certainty that

they had been with humans for at least half a year before being confiscated (Supplementary Table S2, Fig. 3b). Because of the limited sample size in this subset, we included only age at arrival at the station as a predictor. However, separately including potential confounding variables, such as sex or number of cage partners, did not change our results (not shown). Thus, because we also could not find an influence of sex or age when testing curiosity (Table 5), we conclude that individuals that had spent more time with humans before arriving at the rehabilitation station were more curious.

Table 5: Parameter estimates and associated standard errors, obtained from a linear mixed-effects model of PC 1 'curiosity' over 56 'nonwild' individuals

	Estimate	**SE**	***df***	***t***	***P***
(Intercept)	-0.365	0.498	6.50	-0.73	0.489
Sex (male)	-0.011	0.144	48.13	-0.07	0.939
Age	0.001	0.034	37.70	0.03	0.970
Age on arrival at station	0.136	0.048	47.91	2.80	**0.007**
Current no. of cage partners	0.186	0.069	47.31	2.68	**0.010**
Background					
Station/Human vs Unknown	-0.032	0.052	47.25	-0.63	0.529
Station vs Human	0.047	0.115	47.25	0.40	0.684

The model controls for repeated observations on each rehabilitation station (random effect).
$N_{observations}$ = 56, $N_{stations}$ = 3, χ^2= 13.84, *P*= 0.031. Significant *P* values are in bold.

The current number of cage mates also affected curiosity. Since the individuals were mainly placed in groups based on space considerations, this probably reflects a direct effect of sociability on responses to the outside world.

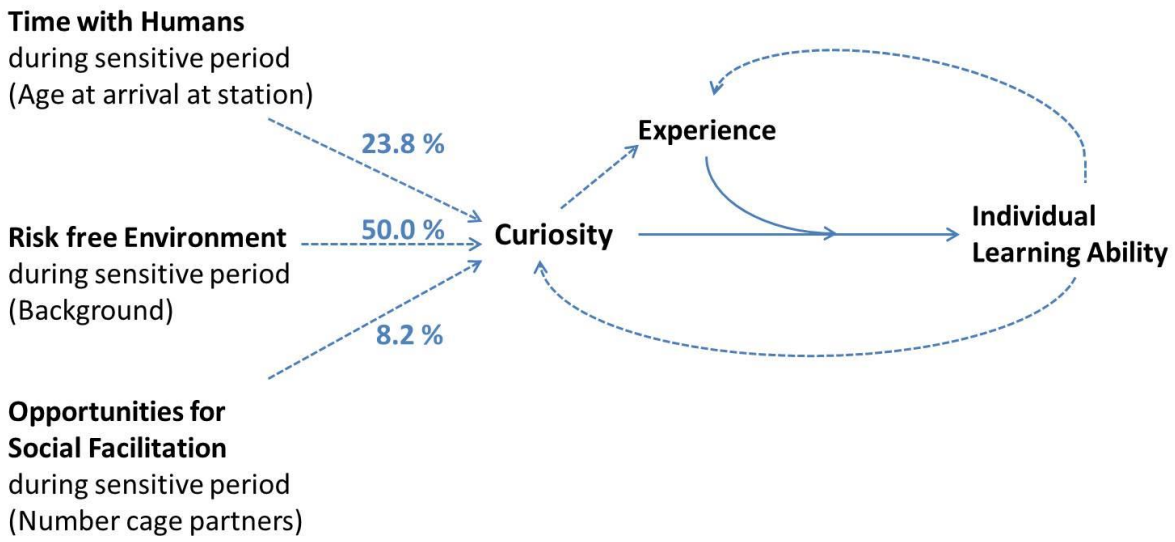

Figure 2: Determinants and consequences of curiosity suggested by the present study. The percentages of variation in curiosity explained by each predictor are shown. The model computed marginal R2 values obtained from LMMs, controlling for repeated observations at different stations. The effects of the predictor variables are not exclusive and may overlap.

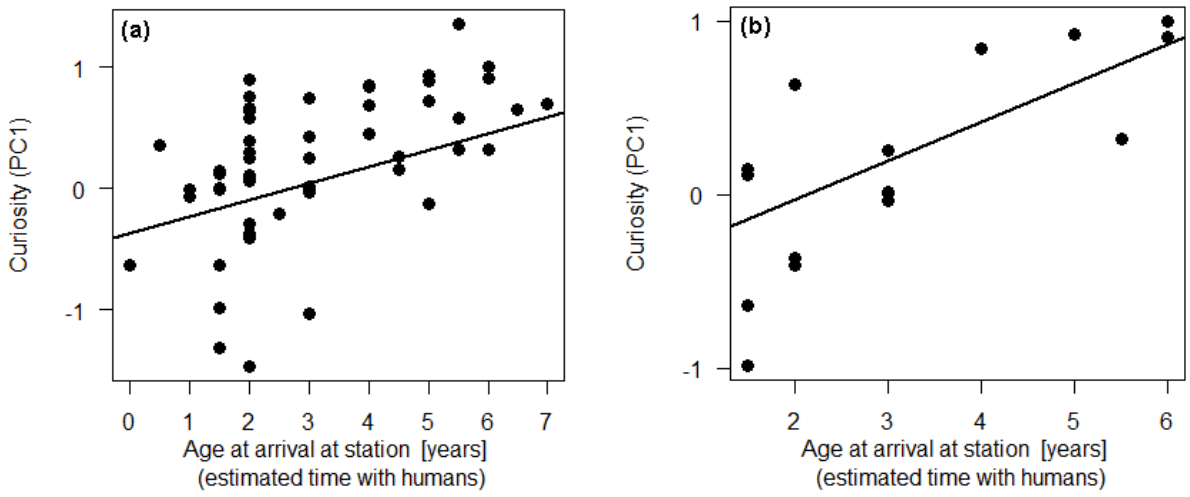

Figure 3: The relation between the individual's age at arrival at the station in years (and thus estimated time with humans) and the PC 1 'curiosity' for (a) the total sample of nonwild individuals (N=56; the fitted line is based on the LMM; see Table 5), and (b) the subsample of 16 individuals certain to have had human contact for at least 6 months (the fitted line is based on the LMM; see Supplementary Table S2).

Determinants of cognitive performance

We next asked to what extent individual characteristics such as age, sex and health, background and response-and-exploration style predicted cognitive performance. Table 6 shows the results of a binomial GLMM of the overall performance including the five different tasks,

predicting the probability of solving the tasks, while controlling for repeated observations in each facility and on each individual. Curiosity was the only significant predictor of cognitive performance (Table 6). The other response-and-exploration style factors (PC 2 and PC 3) had no effect on problem-solving performance. However, the type of task also showed significant effects on performance (Table 6), illustrating that some tasks were more difficult to solve than others, for example the Tube Task (Fig. 4). The Box Task and the Reversal Learning Task exclusively involved natural materials, such as wood, and had a higher probability of being solved when we controlled for other factors including curiosity than tasks that contained artificial materials, such as transparent plastic and metal. This difference suggests that familiarity with materials and their affordances played a role. The Detour Reaching Task, even though including artificial material, was significantly easier to solve than all other remaining tasks (Table 6, Fig. 4). Finally, inserting the stick in the straight channel of the Honey Tool Task was easier than inserting the rope in the curved channel.

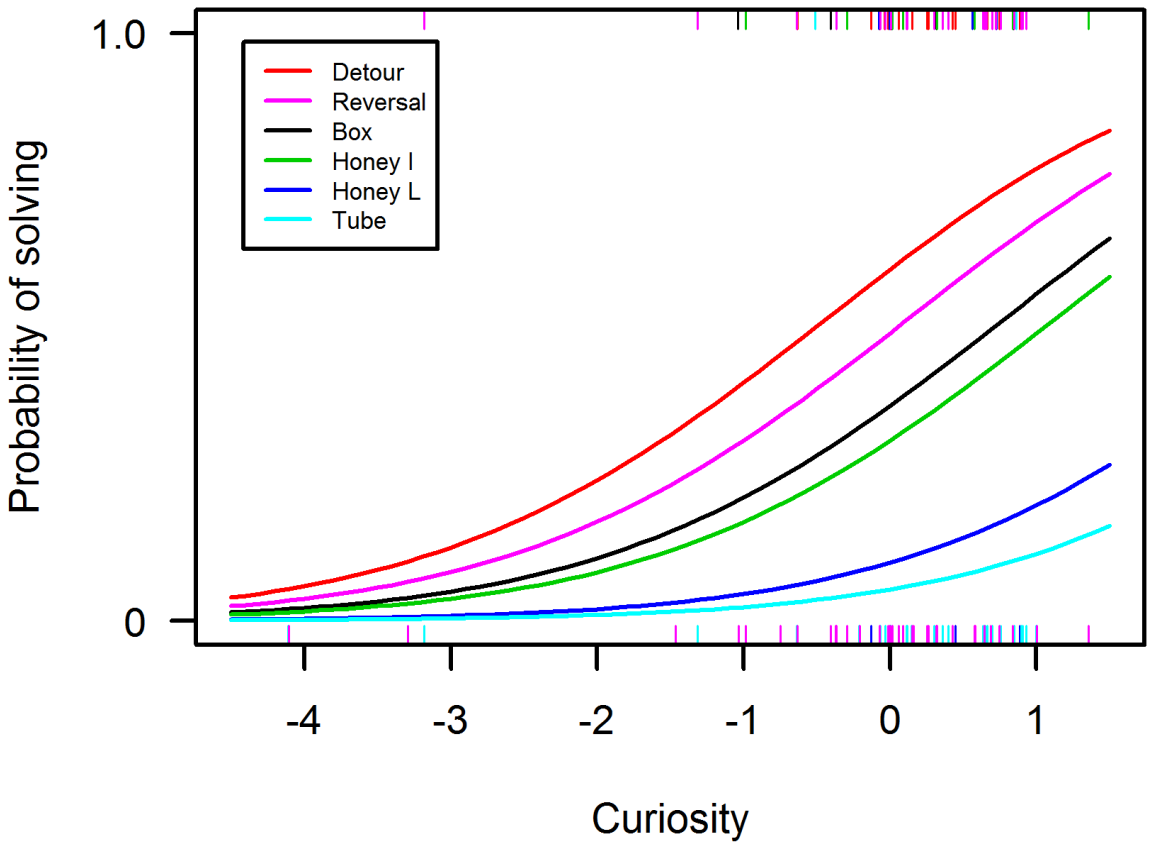

Figure 4: Illustration of the influence of curiosity on the probability of solving each of the five different tasks with six solutions. The rugs along the horizontal axis, below and above, each represents a single data point.

The effect of curiosity on the probability of solving a problem varied significantly (Fig. 4). However, none of the other potential predictors were significant. Thus, the probability of solving the tasks did not depend on a subject's sex, age at testing or its age at arrival, nor on the presence of signs of stereotypies and disabilities or the number of cage partners at the period of the study (Table 6). Neither were there independent effects of island of origin (Sumatran versus Bornean orang-utans), the rehabilitation stations (despite variation in their procedures) or the individuals' background history (Table 6).

Table 6: Parameter estimates and associated standard errors from a binomial GLMM, predicting the probability of an individual solving the task

	B	SE	Lower 95% CI	Odds ratio	Upper 95% CI
Intercept	-0.598	1.04	0.069	0.550	4.521
Sex (male)	-0.037	0.35	0.477	0.964	1.951
Age	-0.015	0.09	0.820	0.985	1.182
Age on arrival at facility	-0.122	0.12	0.687	0.885	1.118
Health characteristic (Yes)	-0.198	0.56	0.252	0.820	2.451
Current no. of cage partners	-0.046	0.20	0.635	0.955	1.440
Facilities					
Sumatra vs Borneo	-0.045	0.27	0.554	0.956	1.644
OCCQ vs NyMen	-0.050	0.40	0.419	0.951	2.094
Background					
Wild vs Others (Station, Human, Unknown)	0.335	0.35	0.696	1.398	2.833
Station/Human vs Unknown	0.055	0.13	0.809	1.056	1.380
Station vs Human	0.124	0.28	0.644	1.132	1.990
Style factor					
Curiosity	0.850	0.34	1.242	2.339	4.825
PC 2 scores	-0.200	0.17	0.577	0.819	1.166
PC 3 scores	0.169	0.19	0.809	1.184	1.745
Task					
Wood vs artificial material	0.606	0.13	1.448	1.834	2.411
Detour vs other tasks	0.430	0.07	1.344	1.537	1.789
Box vs Reversal Learning	-0.283	0.21	0.499	0.753	1.125
Tube vs Honey Tool (IL)	-0.481	0.26	0.329	0.618	0.973
Honey Tool I vs Honey Tool L	0.755	0.31	1.213	2.128	4.144

The model controls for repeated observations at each rehabilitation station and for each individual (nested random effect). The performance in each task was measured in binary fashion, including five tasks with six solutions: Box Task, Detour Reaching, Honey Tool Task stick in the straight channel (I), Honey Tool Task rope in the L-shaped channel (L), Reversal Learning and Tube Trap Task. $N_{subjects} = 61$, $N_{observations} = 358$, $\chi^2 = 78.09$, $P < 0.001$. CI: confidence interval.

Discussion

The aim of this study was to disentangle the determinants of variation in cognitive performance in orang-utans from rehabilitation stations with widely varying backgrounds, so as to identify the experiences that shape the developmental construction of an individual's problem-solving ability. We found that (1) variation in response-and-exploration styles largely reflected the subjects' curiosity, (2) individuals that had experienced long-term social contact with humans (and social housing conditions) were more curious, and (3) more curious individuals were far better at solving novel problems aimed at assessing physical cognition.

What is curiosity?

We assessed the response-and-exploration style through various independent behavioural assays, which revealed that orientation towards humans, a positive response to novelty and a high exploration tendency all share the same underlying latent variable, which we called 'curiosity'. Curiosity explained about a third of the variation observed in the various response and exploration tests. Because two tasks, the HOI and the response to novel food, loaded highly on PC1, they can serve as a quick and reliable estimate of general curiosity in orang-utans. The other PCs did not have any significant effect on problem-solving ability and therefore will not be discussed further.

Our results suggest that curiosity mainly consists of two components: a positive response to novelty and a high exploration tendency. More curious individuals quickly engaged with the novel object/food and showed positive reactions towards a novel human (response style), but they also extensively explored the novel object, doing so gently and with a great variety of actions (exploration style). Therefore, in line with previous definitions in human studies, curiosity reflects the combination of an intrinsic motivation for novelty seeking and a motivation to engage in a diverse array of exploratory behaviours.

What leads to high levels of curiosity?

Humans are likely to exhibit curiosity in an environment with enough resources and free time (Gruber & Davis, 1988; Shalley & Gilson, 2004), leading to the question whether the same circumstances are important for an orang-utan to become curious. Our results (Table 4) confirmed an earlier finding that individuals that had contact with humans early in life showed significantly stronger curiosity than individuals that spent this period in the wild (Forss et al., 2015). Owing to high risks of interacting with unknown environments/objects, wild orang-utans are highly neophobic, but are nevertheless highly motivated to explore once they have overcome

their neophobia, primarily through social information (Schuppli et al., 2016). This reflects the fact that the proximate mechanisms regulating neophobia and exploration are distinct (reviewed in Mettke-Hofmann, 2014), even though in captive animals they end up being highly correlated and thus seemingly part of the same motivational system. Hence, it is not surprising that increased curiosity, so conspicuously lacking in wild orang-utans (Forss et al. 2015, van Schaik et al. 2016), is found among their captive counterparts. As a result numerous innovations can arise in the safe and stable environment of zoos and rehabilitation stations (Lehner, Burkart, & van Schaik, 2010).

The results also suggest that it is not the intensity and nature of human contact per se that is the key factor, but rather the length of stay with humans and especially the age at which this contact occurred, as well as the number of conspecifics the tested individuals were currently housed with (Table 5, Fig. 3). We now examine these effects in turn.

First, the age-on-arrival effect suggests the presence of a sensitive period for the influence of friendly contact with humans on curiosity. Among the 'nonwild' individuals that had contact with humans in the stations or lived with humans before, those that were older when they arrived at the stations were more curious than individuals arriving at a younger age, independent of their age at testing. Because hunters deliberately target young orang-utans because they are more easily handled and more attractive as pets, virtually all individuals confiscated at an older age had had longer exposure to human social-cultural influences. Additionally, none of the individuals arriving at the station were reported as being fearful or aggressive when handled, and therefore had experienced positive contact with humans. Findings on the wild individuals, brought into the stations as adolescents or adults directly after being captured in the wild, support this conclusion of a sensitive period (see also Damerius et al. 2017). They never became curious, even after more time in captivity than the immatures that did become curious. The risk-free environment during a sensitive period in ontogeny and the daily observation of a very broad range of sociocultural interactions with humans and with the artefacts in captivity therefore shaped an individual's response-and-exploration style. Since humans can serve as role models to captive orang-utans this contact might induce loss of both neophobia and the triggering of exploration by social stimuli only.

Second, social learning and social facilitation from conspecifics might have positive effects on curiosity-induced experience. An immediate neophobia-reducing effect of social facilitation is frequently reported among other primate species (Addessi, Galloway, Visalberghi, & Birch, 2005; Forss, Koski, & Van Schaik, 2017; Visalberghi & Addessi, 2000). However, because we tested the subjects individually without conspecifics present, no direct social facilitation was possible during the test. Still, the more conspecifics an individual currently shared its enclosure with the more curious it was. Thus, social contacts during a sensitive period in development can

positively affect the individual's subsequent curiosity, which is then also applied in nonsocial contexts. In chimpanzees, individuals that have spent more time with conspecifics during infancy were more extraverted than individuals that had spent less time with conspecifics (Freeman, Weiss, & Ross, 2016). Recent results from wild orang-utans also suggest that opportunities for social contact during infancy increase subsequent exploration rates (Schuppli et al. 2016).

These findings also help to explain the captivity effect. The safe and protected environment in captivity is likely to quickly erode the strong neophobia found in wild orang-utans. It may also strengthen exploration tendencies, because exploration of novel items usually leads to some reward. Indeed, Damerius et al. (2017) also found that individuals living in zoos and rehabilitation stations were more curious than 'wild' orang-utans, assessed via the HOI, which can serve as a quick measure of curiosity.

We conclude from the comparison between wild and zoo orang-utans that curiosity is elicited by captivity and thus is a major underlying cause of the captivity effect. Similar effects of captivity have also been recognized in other species that can develop curiosity (Benson-Amram et al., 2013; Kronenberger & Medioni, 1985; Tanaś & Pisula, 2011).

Consequences of curiosity

The effects of social interactions, environmental stimulation and experiences during ontogeny on problem-solving success were all indirect: they affected the individual's curiosity, which in turn affects an individual's problem-solving ability. Numerous studies have documented the influences of rearing history and other aspects of biography on social competence and cognition (reviewed in Bjorklund, 2006; Call & Tomasello, 1996; Freeman & Ross, 2014; Freeman et al., 2016; Rumbaugh & Washburn, 2003; Tomasello & Call, 2004), but the present results suggest that these cognitive effects may have been largely mediated through a change in curiosity.

Across all tasks, the probability of solving a task increased with higher levels of curiosity, but the effect of curiosity depended on the type of task. Curiosity was especially effective when solving problems for which trial and error can lead to a solution (e.g. detour reaching). However, highly curious and motivated individuals were not much better than average at solving cognitively demanding problems, which can only be solved after individuals understand the causal structure (such as the tube trap task). Nevertheless, curious individuals may generally be more likely to hit upon the insight needed to solve such problems because they engage more with the problem. In the long run, therefore, the two may interact: although the current level of curiosity and learning ability or insight are independent variables, the accumulated experience due to a long history of curiosity can improve learning ability.

Figure 2 summarizes this idea, by suggesting the following causal links as revealed by the present study. Individuals that are more curious and more open to social interactions with humans and conspecifics garner more opportunities for social learning. First, by seeing human caretakers as trusted role models, immature orang-utans broaden the range of explorable items and contexts. Initially, they probably need direct exposure to human actions, comparable to the triggering of exploration by observing conspecific experts in the wild (Schuppli et al., 2016; van Schaik et al., 2016). Over time, with the lack of negative consequences of being curious, the individuals may come to assume that the mere presence of novel items implies the social approval of the human role model and they might simply respond to all items and contexts they associate with humans. Second, direct social facilitation can also stimulate exploration (Caldwell & Whiten, 2004; Huber, Rechberger, & Taborsky, 2001). Third, individuals are able to gather experience with objects and materials, which is a cumulative process, leading to greater knowledge of affordances and a gradual increase in causal understanding (Byrne, 2016; Greenberg & Mettke-Hofmann, 2001). This latent learning process may further shape the individual's learning ability and curiosity, and the accumulating knowledge can contribute to the acquisition of larger skill repertoires and improved problem-solving ability (van Schaik & Burkart, 2011) and large innovation repertoires, far exceeding those found in the wild (Lehner et al., 2010; van Schaik et al., 2016).

Enculturated apes reflect the maximum extent of these consequences: they were raised in human households with human artefacts and show unusually high social and cognitive skills (Call & Tomasello, 1996). The underlying process may again be their enhanced curiosity. A safe and stable environment when being raised by humans allows them to become highly explorative.

Curiosity and Human Evolution

These results have implications for our understanding of the evolution of intelligence. Humans and orang-utans share the same fundamental phenomena as both are characterized by a slow life history and the presence of tolerant role models during development, which allows for maintaining high neophobia. The unleashing of latent cognitive potential in species that are highly conservative in the wild shows that we should take seriously the possibility that the origin of curiosity may have served as an important contributor to the elaboration of intelligence and culture in modern humans (van Schaik, Forss, & Damerius, 2017). Whereas classic approaches have stressed the importance of brain size and thus individual cognitive capacity, recent approaches have emphasized the role of demographic factors (Henrich et al., 2016) or of improved effectiveness of social transmission (e.g. Pradhan, Tennie, & van Schaik, 2012). The results of this study, however, suggest that curiosity is an additional, potentially important,

nondemographic factor favouring creative innovations and the invasion of novel habitats. Thus, it is possible that a steep rise in innovations had to wait until our ancestors underwent the equivalent of the captivity effect and could afford to become curious explorers in safe conditions and enhanced by social facilitation.

In sum, the results of this study show curiosity to be an important contributor to problem-solving abilities in orang-utans and suggest that curiosity may be an underestimated factor for creative innovations in humans. We should therefore look for indicators of such conditions during hominin evolution. Further work is needed to develop these indicators.

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Chapter 3

General Cognitive Abilities in Orangutans (*Pongo abelii* and *Pongo pygmaeus*)

General Cognitive Abilities in Orangutans (*Pongo abelii and Pongo pygmaeus*)

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For over a century, theories of human intelligence have concentrated on a single general factor, the psychometric *g*, which is used to estimate reasoning ability and cognitive flexibility, i.e. general intelligence. To better understand the mechanisms that favor the evolution of general intelligence, it is important to identify the presence of a psychometric *g* in nonhuman animals, especially in primates, and to further disentangle the influences affecting its development. We therefore investigated the cognitive abilities of 53 Bornean and Sumatran orangutans living in rehabilitation stations, to assess the presence of a psychometric *g* in orangutans, and to explore possible influences on its expression. We did so using a set of carefully selected physical cognition tasks addressing abilities of inhibitory control, behavioral flexibility, causal reasoning, tool use, and associative- and reversal learning in the absence of human experimenters. A principal component analysis of the individuals' performances revealed a first component that accounted for 31% of the individual variation in task performance. Next, we could rule out that this result was an artifact of non-cognitive factors such as health status, island of origin, or rearing background. Finally, we showed that an individual's curiosity positively influenced its *g* score, consistent with the notion that accumulating experience affects the developmental construction of *g*. We conclude that there is evidence for general intelligence in orangutans comparable to humans, and thus suggest evolutionary continuity in this trait.

Introduction

General intelligence in humans can be broadly defined as the ability to show behavioral flexibility, to think abstractly, and comprehend complex ideas; it is thought to be based on reasoning, problem-solving, planning, and learning from experience (Gottfredson 1997). For over a century, theories of general intelligence concentrated on the role of the single general factor, the psychometric *g*, that emerges from factor analysis of the performances across different tasks and domains (Spearman 1904, 1927, Carroll 1993, Jensen and Weng 1994, Jensen 1998).

Although the existence of *g* as a measurable phenomenon of across-domain correlations between diverse mental tests is widely accepted, there is still active debate about what exactly it represents, e.g. whether it is representing a latent variable or rather some emerging property (cf. Burkart et al. 2017), and how *g* is related and contributing to cognitive processes (Conway and Kovacs 2015). Carroll (2003), Geary (2005), Horn and McArdle (2007) argue in favor of either some domain-general ability or a bundle of interacting abilities, which must be highly functionally integrated to be effective (Deary et al. 2016, Burkart et al. 2017). The latter position is consistent with effects of inbreeding or health (Penke et al. 2007, Hagenaars et al. 2016). Regardless of the outcome of these debates, the predictable presence of *g* in broad psychometric studies suggests some system-level property affecting overall cognitive performance across a broad array of tasks.

Some other issues also remain debated. First, there is still some debate about the extent to which socio-cognitive abilities are also correlated with psychometric intelligence; some studies suggest a positive correlation between the two (Baker et al. 2014), whereas others even see socio-cognitive abilities as foundational for intelligence (Estes and Bartsch in press). Second, executive functions, such as inhibitory control, working memory and selective attention, exert top-down control of human adaptive behavior (review: Jurado and Rosselli 2007). There is debate about whether executive functions merely strongly contribute to the shaping of higher cognitive abilities, such as reasoning, problem solving, and planning (Collins and Koechlin 2012, Lunt et al. 2012, reviewed in Diamond 2013), actually coincide with general intelligence (Barbey et al. 2012) or rather be indistinguishable (Royall and Palmer 2014).

Because cognitive abilities are developmentally constructed (Vygotsky 1978), it is often argued that intelligence reflects socio-cultural influences (Neisser et al. 1996, Nisbett 2009, Nisbett et al. 2012, Flynn 2016) and that specific experiences during development may bias the outcome of performance (Reyes-García et al. 2016). These experience effects could also explain the positive relation between motivation, including curiosity and persistence, and general cognitive performance suggested by Gottfried (1990). Depending on how an individual approaches its surroundings, e.g. with high curiosity or great social interest, different learning opportunities unfold. The accumulation of these gained experiences can influence an individual's knowledge and was suggested for the effect of

early novelty seeking in human infants on subsequent IQ (Bornstein and Sigman 1986, Vietze and Coates 1986).

It has traditionally been assumed, mostly implicitly, that general intelligence is unique to humans. However, there is a rapidly expanding literature investigating domain-general abilities in nonhuman animals (reviewed in Burkart et al. 2017). In nonhuman animals intelligence can be defined as the ability to acquire and utilize knowledge to organize effective behavior in both familiar and novel contexts, and thus to behave flexibly (Byrne 1994, Yoerg 2001, Rumbaugh and Washburn 2003).

One major source of evidence in favor of domain-general abilities in nonhuman animals is provided by interspecific patterns, where species differences in cognitive performance on a wide variety of tests are captured by a single variable (Deaner et al. 2006, Reader et al. 2011), to which we refer here as *G* to distinguish it from the intraspecific *g*. Additionally, an increasing number of studies addresses the existence of a psychometric *g* in a variety of different taxa (reviews: Chabris 2007, Matzel et al. 2011, Burkart et al. 2017), including dogs (Arden and Adams 2016), mice (favorite mouse psychometric test Galsworthy et al. 2002, Locurto et al. 2003, Matzel et al. 2003, Matzel et al. 2011, Wass et al. 2012, Matzel et al. 2017) , rats (Anderson 1993), bowerbirds (Keagy et al. 2011), New Zealand Robins (Shaw et al. 2015), cotton-top tamarins (Banerjee et al. 2009), rhesus macaques (Herndon et al. 1997), and chimpanzees (Herrmann et al. 2010b, Hopkins et al. 2014, Woodley of Menie et al. 2015).

Despite the abundance of psychometric studies in nonhuman animals, most have methodological limitations that need to be dealt with before concluding that there is evidence of *g*. There is a serious risk of a false positive result, e.g. because a test-battery is applied where multiple tests all measure similar problem-solving abilities, or because studies do not control for health, motivation and habituation of the individuals (Burkart et al. 2017). Alternatively, the existence of *g* can be masked, e.g. through small sample sizes, or if many tasks are included that are automatized during ontogeny (experience-dependent), and thus form so-called secondary modules (Burkart et al. 2017). Furthermore, as in human studies, we expect the correlations among the performance scores on various tests to be modest, meaning that all animal studies are underpowered (it took massive meta-analyses to convince critics of human intelligence studies: Carroll 1993). Psychometrically identifying *g* in an animal test battery does therefore not *per se* guarantee that this *g* corresponds to general intelligence. Rather, additional validation tests are necessary of the various other correlates of *g*, as done for humans, and to some extent mice (e.g. Matzel et al. 2006, Matzel et al. 2011).

The purpose of this study was to examine the presence of domain-general cognitive abilities in orangutans and to link it to biological, social and developmental features. Orangutans are good candidates for such a study. They are Asian great apes known for advanced cognitive abilities, such as flexible tool use (van Schaik 2004), planning (van Schaik et al. 2013) and large innovation repertoires in the wild (van Schaik et al. 2006), as well as problem-solving abilities in zoological gardens (Lethmate 1977, Lehner et al. 2011). Orangutans also show extended development and a long phase of socially mediated learning (Schuppli et al. 2016a) to acquire their geographically variable skill

repertoires (van Schaik et al. 1996, van Schaik et al. 2003, Jaeggi et al. 2010, Schuppli et al. 2016b), consistent with the possibility that intelligence is developmentally constructed under the influence of a variety of inputs and experiences.

The first aim of this study was to explore the possible presence of a psychometric *g* in a large sample of orangutans, by investigating a broad array of problem solving-abilities from a test battery of five different physical cognition tasks. It is important assess this in orangutans, because results are mixed for the only other great ape species for which psychometric *g* studies have been conducted, the chimpanzees. Hermann et al. (2010) did not find a *g* in chimpanzees within a sample of 106 individuals over multiple social and non-social tasks. Their factor model described two distinct areas: the spatial and the physical-social area. Hopkins et al. (2014), in contrast, derived a factor representing *g* using a broad intelligence battery based on similar methods (Herrmann et al. 2007) with 99 individuals. Woodly of Menie et al. (2015) reanalyzed the same dataset and confirmed the presence of *g* in chimpanzees. Given the fact that chimpanzees are our closest living relatives, these mixed results call the presence of *g* in great apes into question, and studies investigating *g* in another great ape species, such as the orangutans, are crucial.

The tasks in this study were very carefully selected to minimize overlap in their domains, to exclude confounding motivational influences, and to represent abilities that are similar in humans. These tasks also included tests of inhibitory control to assess the correlation between domain-general cognitive abilities and executive functions found in humans. Importantly, to prevent any bias in favor of individuals familiar with humans (see also Schubiger et al. 2015), unlike in previous studies with primates, no experimenter was present during testing.

Because of the risk of false positive, finding a structure indicating a single component with significantly shared variance across the tasks is necessary for showing the presence of general intelligence, but not sufficient. We therefore conducted a series of additional validation tests to evaluate this preliminary conclusion. First, we asked whether the potential orangutan *g* could be an artifact of alternative non-cognitive factors possibly generating false positive results, such as health, sex, rearing background, and island of origin of the individuals. Second, because general intelligence is highly responsive to early conditions, we looked for effects of experience, assessed through an individual's curiosity and social interest. If a curious problem-solving approach and high social interest lead to greater knowledge and experience when sustained throughout life, we expect curiosity and social interest to be positively linked to a possible *g.* A positive relation between individuals' curiosity and their physical problem-solving abilities was recently shown in orangutans (Damerius et al. in review), suggesting that curiosity might indeed channel the prospecting of novel social and physical challenges that can lead to quantitatively and qualitatively different learning opportunities over lifetime (Byrne 2016, Damerius et al. in review). Finally, we asked whether social interest predicted performance on the test battery.

Methods

Study Subjects and Species

The study included 40 Bornean (*Pongo pygmaeus wurmbii*) and 13 Sumatran (*Pongo abelii*) orangutans housed at rehabilitation stations in Indonesia, of which 23 were females and 30 males (see Supplementary Table S1, category Data Set: conservative). In order to be able to disentangle the actual cognitive abilities from motivationally driven performance, we only included subjects who passed the criterion of having touched all tasks at least once. This resulted in a conservative sample size of 53 individuals with no missing data point over all five tasks. (In the Supplementary Material we present an analysis of the extended data set of 57 individuals, which also includes the four individuals that participated in only four out of the five tasks [Table S1, category Data Set: extended], and show that the results are very similar).

The individuals varied in background, although all were wild-born (see Supplementary Table S1). We distinguished four categories of individuals. The first category ('human') included individuals, who had stayed with humans for at least six month and were subsequently brought to the rehabilitation station. The second category ('station') included those who had arrived at very young ages (<1.5 years old) and essentially grew up in the rehabilitation station. The third category ('wild') where those who were rescued when their habitat was lost to conversion and brought directly to the station; these individuals were already older at arrival. Finally, we also had individuals whose the background was unknown ('unknown'). Further information on the classification can be found in Damerius et al. (in review). This heterogeneity of background experiences of the individuals allows us to examine experiential influences on *g.*

The subjects' ages at testing ranged from 3.5-17 years (Supplementary Table S1). Their ages had been estimated upon arrival by the staff of each facility based on dental eruption patterns.

Study Facilities and Housing

LD, a colleague (Zaida Kosonen), and a trained assistant (Andreas Wendl) collected the data between June 2012 and June 2014 in four facilities of three organizations across Sumatra and Central Kalimantan, Borneo. We used the same experimental tasks and procedures in every facility with minor modifications of the presentation table that had to be adjusted to fit the conditions of each facility.

Sumatran Orangutans (*Pongo abelii*) **1.** Quarantine station in Batu M'Belin (QBM), Medan, North-Sumatra of the Sumatran Orangutan Conservation Program (SOCP): 8 subjects were part of our study (2 females, 6 males). Their ages ranged from 5 to 10 years and we tested them in their home enclosures, as they were housed alone. **2.** Release Site Danau Alo, Bukit

Tigapuluh, Jambi, Sumatra. The release site belongs to SOCP. Five solitarily and social housed subjects (4 females, 1 male) with ages between 3 – 6 years were part of our study.

Bornean Orangutans (*Pongo pygmaeus*) **3.** Orangutan Care Center and Quarantine (OCCQ) in Pasir Panjang, Central Kalimantan: This facility is managed by the Orangutan Foundation International (OFI). The 26 subjects' ages ranged from 8 to 14.5 years, with 10 females and 16 males. Testing occurred in external test cages, since all individuals were socially housed in peer-groups of equal sex ranging from 2-6 individuals. **4.** Nyaru Menteng Rescue Center, Palangka Raya, Central Kalimantan: This rehabilitation station is managed by the Borneo Orangutan Foundation International (BOSF). We tested 14 subjects (7 female, 7 males) in their home enclosure with an equal number of both sexes and between the ages of 6 to 17 years.

In order to prepare the orangutans for release, the stations limit contact with humans apart from routine check-ups by veterinarians and cage cleaning and feeding by caretakers several times a day. In the Bornean facilities, individuals that arrived as very young dependent immatures were placed in the station's nursery, where human caretakers served as replacement mothers. The infants received close physical care and supervision together with other infants of their age. In Sumatra, arriving dependent infants are introduced to peer groups after quarantine. All individuals on both islands had simple enrichment devices installed in their enclosures, such as tires, ropes and platforms. All stations offered food-related enrichment several times a week and depending on the age and stage of rehabilitation most individuals received regular forest walks.

Physical cognitive test battery and procedure

A test battery of five different physical cognition tasks was developed for measuring problem-solving abilities: the Box Task, Detour Reaching, Tube Trap Task, Honey Tool Task and Reversal Learning. These five tasks were meant to cover distinct cognitive abilities, namely flexibility response, inhibition, causal reasoning, tool use, and reversal learning, including associative learning and memory. We focused on performance measures that best reflected possible components of domain-general cognitive processes, and thus avoided measures that might reflect success based on trial-and-error exploration. We aimed at applying various tasks of different cognitive domains, to minimize the risk of re-sampling the same cognitive domain repeatedly, which would result in a first PC that represents this specific domain, instead of being consistent with domain-general abilities.

The experiments required no pre-training and, with the exception of the Tube Trap Task and Reversal Learning requiring multiple sessions, were presented only once, in a random order, on consecutive days and on a specially designed presentation table (Supplementary Fig. S1). The individuals were able to interact on a voluntarily basis with the apparatus since it was presented from the outside of the enclosure. This way, the individuals were able to reach through the mesh or bars to freely explore the apparatus. To prevent a bias in favor of orangutans familiar with humans, no human

was present during testing. Whenever possible, a familiar caretaker helped to prepare the set-up of the apparatuses outside the view of the enclosures. The caretaker and the experimenter left the testing area once the apparatus, the presentation table and the cameras had been prepared.

The following experiments were part of the cognitive test battery:

1) Box Task: Flexibility

The experiment allowed us to assess the cognitive skills of associative learning and flexibility. The task consisted of two consecutive presentations of five identical wooden boxes, each with a lid and a sliding door (Supplementary Fig. S2). Learning phase (4min): During the first presentation the lid of all five boxes could only be opened by flipping. Individuals learned that they could flip open the box in order to receive the bait, a peanut. When four out of five boxes were flipped open the criterion for learning had been fulfilled and the second condition of the task was presented. All individuals included in this sample passed the Learning phase. Flexibility phase during second presentation (7min): Immediately after passing the Learning phase, the lids were locked, the sliding doors were unlocked and the boxes baited again out of view of the subject. The previously learned solution had thus become non-functional and the subjects needed to explore to find the exclusive solution of opening the sliding door to gain access to the peanuts in the boxes. The performance measure was the number of opened boxes in the flexibility phase.

2) Detour Reaching: Inhibitory control

The Detour Reaching experiment is a classical inhibitory control task and serves as a key predictive measure of problem-solving skills in human and nonhuman animals (Carlson and Moses 2001, Vlamings et al. 2010, Amici et al. 2012). A transparent Makrolon box that had two openings at the front, a small one on the right-hand side and a large one on the left-hand side, was presented to the individuals for five minutes (Supplementary Fig. S3). A preferred fruit/enrichment object that was too big to fit through the small opening was placed in the box directly behind the small opening. The subject could not reach for the object directly through the small opening, but could reach for it through the large opening. Therefore, the individual had to inhibit grasping for the putative direct solution and reach around (making the detour) to retrieve the reward. The performance measure was the latency from first touching the apparatus (the moment the individual began to engage with the test) until exploring the box side of the large hole for the first time.

3) Tube Trap Task: Causal reasoning and Learning

Causal reasoning and learning ability were needed to successfully solve the Tube Trap Task, which was inspired by Visalberghi and Limongelli (1994). It consisted of six horizontally

placed tubes with open tube ends but an opaque trap situated either left or right from the center. The tubes were mounted on a vertical board (Supplementary Fig. S4). The front of the tubes was transparent and contained a slit wide enough for an orangutan finger to slide food inside the tube. This slit extended along the entire length of the tube so that the subjects could slide the food reward to the left or right tube opening. However, if the food was moved in the direction of the trap, the food fell through a hole into the opaque trap, and could no longer be retrieved (Supplementary Fig. S4,a). The task for the subjects was to learn this causal relation and to slide the food in the correct direction (Supplementary Fig. S4,b). The board with the tubes was presented to the subjects three consecutive times for 4 min each. The subjects were given the possibility to explore a total of 18 randomly distributed tubes to learn to avoid the trap. The performance measure was the number of rewards retrieved over all three trials.

4) Honey Tool Task: Goal directed tool use

This task assessed physical cognition and the ability to use tools, as well as the ability of causal reasoning to select the correct tool. The subject was presented with the opportunity to fish for honey out of two channels; therefore the task had two possible solutions. The apparatus consisted of a wooden box with two embedded transparent Makrolon tubes: a straight channel and a curved L-shaped channel. The front was covered with a Makrolon plate to ensure stability and a good visibility into the tubes that were baited with honey (Supplementary Fig. S5). The subject was offered two different types of tools to use for honey fishing: three long sticks (40 cm), one of which was already inserted in the straight channel, and three ropes (20 cm). With the help of the sticks, honey could be reached in the straight channel, but the stick could not be bent in the curved channel. Whereas the rope was too short for the straight channel, it flexibly fitted into the curved L-shaped channel. Both channels were too long for an orangutan's finger to reach the honey.

We could use an ordinal scale to measure performance, because the data fitted a Guttman scale, which showed a reproducibility coefficient close to one (0.92), with 71% individuals completely fitting the applied Guttman scale (listed from simplest to most complex). The following scores were used: 1) inserting finger in either of the channel, 2) tracing the honey in channel from outside (revealing their understanding that there is honey insight), 3) inserting tools in either of the channels, 4) goal-directed tool use outside (directly aiming for the honey with the correct tool), 5) successfully dipping and feeding on honey with stick in straight channel, and 6) successfully dipping and feeding on honey with rope in curved channel.

5) Reversal Learning: Associative and reversal learning

Reversal learning is a widely used paradigm for determining cognitive flexibility (reviewed in Izquierdo et al. 2016). It assesses associative learning and reversal learning abilities. At first the subjects learn that one possible combination of two stimuli (location, color) is linked to a reward whereas the second one is not. Once the individual has associated the first stimulus with the reward the contingency is reversed and the first stimulus no longer indicates the reward, but now the second one does. In the current study the subjects were presented a board with square black and round white doors on either side of the presentation board (Supplementary Fig. S6). The doors could be swung open by turning them to the right or to the left and gave way to a hollow space. A randomly determined side was baited behind each door in the depository space with a preferred food item, e.g. a peanut. Therefore, when the subject opened a baited door, it was rewarded. The task for the subject was to learn the association between food and location, which was enhanced by the different colors and shapes of the doors. If the subject opened at least five out of the first six doors at the correct location on two consecutive trials, it had fulfilled the criteria for learning. After the location of food was accurately associated, we tested the stability of the result by applying a reminder test the next day. Subsequently, the location of the reward was switched to the other location in order to test for reversed learning, where the same criterion of at least 5 out of 6 correct choices was used. The board was presented for 4 min per trial, with three to four consecutive trials per day (in total up to 16 min/day). The Reversal Learning board was presented to the individual for a maximum of 4 days.

We constructed an ordinal scale to measure performance on the three consecutive components: learning, memory and reversal learning. Individuals that did not achieve learning received a performance score of 0, individuals that were able to learn but failed subsequent tests a 1, individuals that were able to learn and remember a 2, and individuals that were able to learn, remember and learn the reversal a 3.

Measurements of experiential effects

In addition to the cognitive tasks, we carried out independent tests to assess individual variation in experience, such as curiosity and social interest. Each individual's level of curiosity was assessed through five different tasks, including a novel object test, human orientation tasks, reactions toward a snake predator model and reactions to both familiar and novel food. Each task lasted two minutes and was presented separately from the outside of the enclosure without any experimenter present. A principal component analysis of these measures yielded an individual's curiosity score. Damerius et al. (in review) provide a detailed description of the tasks to estimate curiosity and the PCA analysis.

One station had the logistics for testing the subjects' social orientation toward conspecifics (n= 26 subjects) in external testing cages. The social orientation task lasted for 15 min. When an individual arrived in the test cage, it could choose between two compartments: a social one, with visual access to a neighboring compartment with familiar same-sex conspecifics, and an asocial compartment. We measured the proportion of time individuals spent in the compartment with visual social access, as a measure of the individual's social interest.

Data extraction and statistical analyses

All experiments were videotaped with two Sony camcorders (HDR-CX200 high definition handycam 5.3 MP). The video footage was imported into the program Interact, version 9.7.5.0 (© Mangold International GmbH) for transformation and coding of the cognitive performance by LD. Data on exploration and novelty responses were also coded by LD, apart from social interest and some tasks used to generate the curiosity score, which were coded by a trained assistant (Anna Schöpfer). LD and the assistant independently coded 21% of the videos and came to a good inter-rater agreement (Cohen's Kappa: 0.701; N responses= 185, P <0.001).

First, we used descriptive statistics (means with standard deviation or medians with minimum and maximum values) on the five task-specific cognitive performance scores to explore the distribution of the variance in performance (Table 1). The signs of latencies of the Detour Reaching Task were reversed for the model to represent the ability of inhibitory control.

Second, we calculated Spearman-Rho correlations to estimate the relationships between the different five measures of cognitive performance from the five different tasks. We applied Bonferroni corrections on the level of 0.01 ($\alpha/N=.05/5$).

Third, in order to investigate the psychometric structure we applied an unrotated principal component analysis (PCA) on the five performance measures (Table 1), for both, the conservative and extended data set (see Supplementary Table S1). The PCAs were conducted in *IBM SPSS Statistics*, version 22.0.0.0 (© IBM Cooperation and other(s), 1989, 2013). This PCA method was chosen to answer the primary question, i.e. whether there are across-domain correlations, shared variance, between the diverse performance measures and to how many components the cognitive domains can be reduced.

Additionally, to assess whether the performance variable's distribution affected the outcome of a psychometric structure of *g*, we ranked each subject's performance within any given task and performed an additional PCA (presented in the Supplementary Material). Subjects with the best performance received the value '1' whereas subjects with the lowest performance the rank of '53'. Tied performances were given equal scores, such that the median value was returned (overview of measurements see Supplementary Table S2). For additional investigations if the factorial method used showed an effect, we conducted an exploratory factor analysis (EFA) in *JMP*, version 12.1.0 (© 2015

SAS Institute Inc.) using maximum likelihood estimation (ML) on the five performance measures (Table 1).

The following statistical analyses were performed in *R* version 2.1 (R Core Team 2016) using the 'lme4'(Bates et al. 2014) and 'multcomp' packages (Hothorn et al. 2016).

Fourth, we used Linear Models (LM) to investigate whether variation in the first principal component (PC1), can be explained by non-cognitive factors such as health characteristics, species (island of origin), background, sex or age. The contrasts for the categorical predictor variables *Background* was specified *a priori* to explicitly compare wild individuals toward all others, individuals with 'unknown' background toward the 'station' and 'human' backgrounds, and the direct comparison between 'Station' and 'Human' backgrounds. Further possible experiential effects, such as an individual's social-interest were investigated with a LM in a subsample of 26 individuals.

Finally, to assess additional experiential influences on the PC1, we used univariate Linear Mixed-Effects Models (LMM) with age and curiosity as fixed effects, the different rehabilitation stations and backgrounds as random effects, and the first principal component as a response. The LMMs were first performed on the complete data set (N=52) and secondly on a reduced data set of only non-wild individuals N=50.

Ethical note

The experimental protocols were in full compliance with the Swiss Animal Welfare legislation and were approved by the Indonesian ministry of research and technology, RISTEK. They also fully complied with ethical guidelines of each facility and followed the International Primatological Society's Ethical Standards for Research on Nonhuman Primates.

Results

Variation in cognitive performance

Table 1 shows the overall level of task performance in the five tasks of the test battery. There was high variance within all of the task performances and importantly neither floor nor ceiling effects were present.

Table 1: Description of tasks and measurements

Cognitive ability tested	Task administered	Performance measurement	Measurement description	Mean (SD) or Median (min/max)	N
Flexibility	Box Task	Quantity	Number of boxes opened (max: 5)	3.02 (1.67)	53
Inhibitory Control	Detour Reaching	Latency	Latency to exploration of the non-food side (max: 300 sec.); since short latencies represent better task performance, latencies were reversed for the model to represent the ability of inhibitory control	70.86 (91.95)	53
Tool use	Honey Tool Trap	Levels of solving	Guttman scale of goal directed tool use (max: 6)	3 (0/5)	53
Learning Remembering Reversal Learning	Reversal Learning	Levels of solving	Level of achievement on learning, remembering, and reversal learning tasks (max: 3)	2 (0/3)	53
Causal Reasoning	Tube Trap Task	Quantity	Number of rewards retrieved in all three trials (max: 18)	6.698 (3.30)	53

Relationships between the different tasks

Consistent with findings of previous human studies (Carroll 1993), the majority of individual task performances were positively correlated in a pairwise comparison over all tasks (Supplementary Table S3). The ability of Learning, Remembering, Reversal Learning was weakly correlated with the ability of Causal Reasoning (*Spearman-Rho*, r= .333, P=.015, N=53) and Flexibility (*Spearman-Rho*, r= .247, P<.074, N=53). After Bonferroni correction (at a significance level of p< .01 [α/N=.05/5]), none of the correlations remained significant. There was one, very weak, negative correlation between Tool Use and Learning/Remembering/Reversal Learning (*Spearman-Rho*, r= -.028, P=.932, N=53), indicating little cognitive overlap between these abilities.

Principal Component Analysis

Across the five different cognitive tasks, the potential overlap of the cognitive performances was assessed using an unrotated Principal Component Analysis (PCA). We found that 52.35% of the variation in orangutan performance is regulated by two components that were extracted with significant eigenvalues greater than 1 (Table 2). Item loadings greater .50 were considered salient. The first component accounted for 31.28% of the variance in task performance over all 53 individuals.

All tasks loaded positively on the first component. Especially the three domains of Reversal Learning Task (Learning, Memory and Reversal Learning), Causal Reasoning, and Flexibility attained high scores on the first component, followed by the ability of Inhibitory Control. This domain-generality of the first component is one of the most important criterion for detecting *g* (Carroll 1993), but further validation is necessary to for fully identifying the presence of *g.* We therefore for now refer to this component as the potential *g.*

The second component, which explained 21.07% of the variance, had strong loadings from *Tool use* and *Inhibition* and we refer to it as *Tool Use Ability*.

Similar results were obtained when performing a PCA with the extended data set of 57 individuals (Supplementary Table S4), which included four imputed data points (Supplementary Table S1, category Data Set: extended). In addition, in order to investigate whether the variable distribution or the factorial method chosen affected the outcome of the *g* analysis, we performed two parallel analyses on the conservative dataset: an unrotated PCA with ranks applied, and an exploratory factor analysis (EFA). In both analyses, the results of the first component or factor are very similar in their magnitude and orientation of the item loadings (see Supplementary Tables S5 and S6). The main difference was that the percentage of shared variance for *g* was slightly lower in the EFA; this difference between EFA and PCA is not surprising considering their different communality estimates, the low number of variables (respectively for statistical methods), and low communalities (<0.4) of the sample (but see Stevens 2002, Field 2013 p. 638).

Table 2: Principal Component Matrix with Component Scores and Item Loadings of the five problem-solving domains

Item	Item Loadings	
	***g* (PC1)**	***Ability of Tool use* (PC2)**
% of variance	31.28	21.07
Eigenvalues	1.56	1.05
Learning & Remembering & Reversal Learning	**.755**	-.360
Causal Reasoning	**.665**	-.118
Flexibility	**.513**	-.198
Inhibitory Control	.451	.485
Tool use	.292	**.797**

Note: N = 53, Rotation = none. PC=Principal Component Component loadings > .50 appear in bold

PC1 scores and non-cognitive factors

We next tested whether alternative non-cognitive factors possibly explain the PC1 scores, the potential *g*. Table 3 shows the results of a Linear Model of the PC1. Because the sample size did not allow us to include all independent variables of interest, such as health deficits, such as loss of hair or stereotypical behavior patterns, we repeated the analysis with health deficits included, instead of age (Supplementary Table S7). All analysis and other combinations of replaced variables (not reported here) showed similar robust results. First, there was no significant effect of age. Second, individuals with visible health deficits did not score significantly lower on the PC1. Likewise, we found no influence of background conditions (wild, time with humans as pets, grown up in station, unknown), no differences between the sexes, or between the two different islands. However, we did find differences between the rehabilitation stations (Fig. 1; Estimate ± SE= -0.451±0.18, P=0.016), specifically between the Bornean stations (for reasons of confidentiality we refer to them as Bornean 1 and 2). Overall, we found no effects of age, sex, health, island, or rearing background on performance on the cognitive tasks, but noticed that current management regimes did affect PC1 scores.

Table 3: Linear Model of PC1 *(g)*, N=53

	Estimate	***Std. Error***	***P value***
(Intercept)	-0.105	0.65	0.874
Age	0.023	0.06	0.706
Sex (male)	-0.034	0.27	0.902
Background			
Wild vs. Others	-0.059	0.18	0.740
Others vs. Unknown	-0.032	0.10	0.762
Station vs. Human	0.103	0.23	0.655
Rehabilitation Station			
Sumatra vs. Borneo	0.238	0.16	0.153
Borneo 1 vs. Borneo 2	-0.451	0.18	**0.016 ***

Note: F-statistic: 2.263 on 7 and 45 DF, P<.05

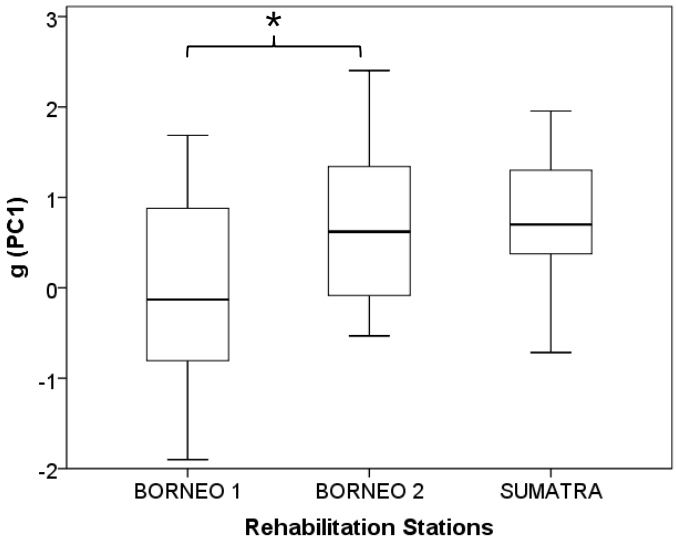

Figure 1: Individual's the potential *g* (PC1) scores differed significantly between the two Bornean rehabilitation stations (-0.451±0.18, P=0.016)

Experiential effects on PC1 scores

We aimed to investigate whether experiential effects have an influence on the development of the possible domain-general ability captured by PC1. In particular we were interested whether an individual's approach toward conspecifics and novelty, possibly resulting in different individual experiences when maintained during ontogeny, affects the potential *g*. Therefore, we first tested over 52 orangutans (one individual had no curiosity score) the influence of curiosity on PC1, when controlling the linear mixed effect model for other potential experiential effects such as age, background history and different rehabilitation station (the two latter are included as random effects). Curiosity did not predict PC1 scores (Table 4).

Table 4: Parameter estimates and associated standard errors, obtained from a Linear Mixed-Effects Model of PC1 *(g)* over all 52 individuals

	Estimate	***SE***	***df***	***t value***	***p value***
(Intercept)	0.028	0.64	7.83	0.04	0.966
Age	0.007	0.05	18.85	0.13	0.896
Curiosity	0.193	0.18	48.50	1.07	0.292

Note: The model is controlling for repeated observations on each rehabilitation station and background (random effects). N observations = 52, N stations = 3, N background = 4

Because wild individuals were in general far lower on curiosity (Damerius et al. in review) and one wild individual produced a highly significant outlier (with a curiosity score of -3, see Supplementary Fig. S7), we repeated the analysis for non-wild individuals. Within the sample of the remaining 50 non-wild individuals, an individual's curiosity positively influenced PC1 scores (the

potential *g)* in orangutans (Estimate ± SE= 0.541±0.26, P=0.0467, Table 5, Fig. 2). Therefore, non-wild individuals that were currently novelty-seeking and highly explorative showed significant higher *PC1 scores* than individuals that were not (Fig. 2).

Table 5: Parameter estimates and associated standard errors, obtained from a Linear Mixed-Effects Model of PC1 *(g)* over 50 non-wild individuals

	Estimate	***SE***	***df***	***t value***	***p value***
(Intercept)	-0.153	0.60	5.27	-0.26	0.807
Age	0.012	0.05	9.32	0.22	0.829
Curiosity	0.541	0.26	44.57	2.05	**0.0467 ***

Note: The model is controlling for repeated observations on each rehabilitation station (random effect). N observations = 50, N stations = 3, N background = 3
*Statistical significance is indicated as follows: *P< 0.05*

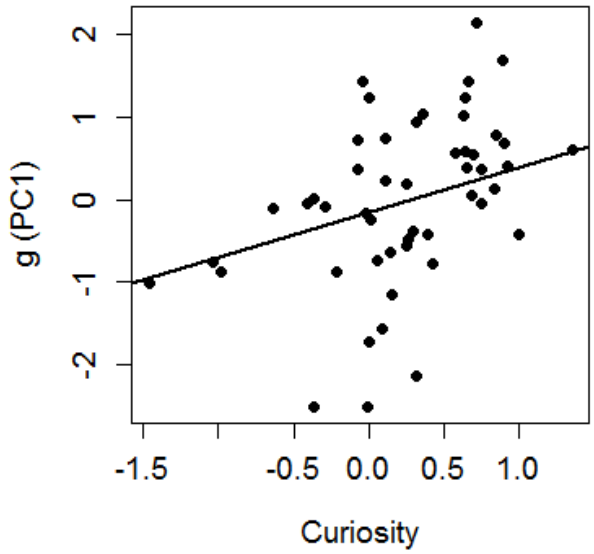

Fig. 2: The relation between curiosity and the potential *g* (PC1) plotted with a fitted line based on the LMM (see Table 5) within all non-wild individuals (*N=50*).

Secondly, we examined in a subsample of 26 Bornean orangutans whether an individual's social interest affects their PC1 scores, presuming that a higher social interest leads to more opportunities of social learning and consequently influences cognition development. The Linear Model, controlling for sex and age, showed no experiential effect of social interest on PC1 scores, the potential *g* (Table 6). The experiences gained from current social interest in conspecifics might therefore not directly contribute in shaping the potential *g.*

Table 6: Linear Model of PC1 (*g*), N=26 (Bornean orangutans)

	Estimate	***SE***	***P value***
(Intercept)	-0.135	1.794	0.941
Social Interest	0.001	0.001	0.280
Sex (male)	-0.078	0.493	0.876
Age	-0.066	0.151	0.669

Note: F-statistic: 0.4804 on 3 and 22 DF, p> 0.5

Discussion

We investigated the cognitive abilities of 53 Bornean and Sumatran orangutans by comparing their performance over multiple physical cognition tasks addressing abilities of inhibitory control, behavioral flexibility, causal reasoning, tool use, and reversal learning, including associative learning and memory. Individual performance on these tasks was generally positively correlated across these tasks, and an unrotated principal component analysis indicated that the first component accounted for 31% of the individual variation in task performance of orangutans. Our findings of this specific psychometric structure are generally in line with previous findings in nonhuman animals (e.g. Herndon et al. 1997, Matzel et al. 2006, Hopkins et al. 2014).

Although the five physical tasks of the test-battery were designed to measure independent abilities and minimize the transfer of experience between the tasks, one first component explained a third of the variance in individual performance. The responses toward associative learning, memory, reversal learning, causal reasoning, and behavior flexibility all loaded positively on the potential *g* (Table 2). Successful individuals must have been therefore capable of learning, but also open to novel information and to flexibly reuse this information to relearn new associations.

In humans the abilities of flexibility and inhibitory control are considered an expression of executive functions, which importantly contribute to shaping higher cognitive abilities, such as reasoning and problem solving. Our findings show that they both abilities also load positively on the first component, i.e. share variance with *g.*

Overall, the structure of cognitive abilities in orangutans is therefore comparable to that found in humans. This conclusion is based on a small number of tests. However, we focused on highly conservative measures to minimize possible statistical dependencies. For instance, the reversal-learning test contains three phases, which have nearly independent components and provides additional information about performance. Thus, if we include associative learning as a separate measure into the principal component analysis to additionally consider the quality of learning and not only whether they learned or not, we find that the loadings remain quite similar (Supplementary Table S8). This result, taken together with the facts that a PCA based on ranked data and the EFA yielded highly similar results (Supplementary Tables S5 and S6), thus shows that the PCA results are robust.

The ability to effectively use tools loaded highly on a second principal component (Table 2). This is consistent with the fact that tool-use abilities are prone to be automatized during ontogeny, representing so-called secondary modules that are experience-dependent (Burkart et al. 2017).

Because finding the positive manifold merely constitutes a necessary, but not sufficient condition, for demonstrating the presence of *g* in orangutans, we also investigated whether the present structure of performance was due to confounding artifacts. We did not find that possible non-cognitive variables, such as sex, health, background and origin, affected the PC1 and therefore exclude an artificial rise of a psychometric structure consistence with *g* due to these variables. The one exception was an effect of the different management regimes at the stations, which we believe is of different origin, as discussed below.

Because all these analyses are consistent with the interpretation of PC1 as reflecting domain-general abilities, we conclude it is justified to refer to it as *g*. In what follows, we focus on the role of experiential factors, such as curiosity, for the construction of *g* during development and the possibility of an evolutionary continuity of domain-general processes.

Experience Effect and developmental influences on g

Previous studies suggested that curiosity underlies problem-solving performance in orangutans, especially in tasks where trial-and-error exploration, rather than causal comprehension, facilitates finding a solution (Damerius et al. in review). The results of this study show that curiosity is also positively linked to *g* (Table 5; Figure 2), consistent with the presence of domain-general cognitive abilities.

The mechanism underlying this relation warrants discussion since curiosity merely consists of a positive response to novelty and a high exploration tendency (Damerius et al. in review), and a curious problem-solving approach will therefore not necessarily make an orangutan instantly cleverer. Only when this approach is maintained during life time resulting in different opportunities for learning, this cumulative experience effect can in the long run affect an orangutan's general abilities and vice versa. Discrepancies of the *g* scores between the Bornean stations (which hosted the same sub-specie *Pongo pygmaeus wurmbii*) in all likelihood reflected these differences in opportunities for learning (Fig. 1).

Interestingly, in the tested subsample of 26 Bornean orangutans, we did not find a direct relation of social interest and *g*, even if an individual's social interest should play an important role for the opportunities of social learning and the construction of cognitive abilities (van Schaik and Burkart 2011). The small sample size and much uncontrolled variation in individual experiences during ontogeny possibly influencing *g* (each individual had its own history before arriving at the station) make it difficult to disentangle the pure influence of social interest. This cumulative experience effect might also explain why we did not find differences between the two species, although intrinsic differences in the ability of cognitive performance between Sumatran and Bornean orangutans at

zoological gardens (kept under virtually identical social and physical conditions) have been reported (Forss et al. 2016). Since individuals living in rehabilitation stations vary greatly in their background and previous experiences, including possible traumata, far more so than any captive zoo orangutan, it is possible that the intrinsic island differences were masked by different experiences and circumstances during ontogeny. However, it is also likely that the expression of orangutan cognitive abilities, represented by *g*, itself is independent of genetic prepositions between the species, but might reflect the inherited differences of an individual's curiosity. If so, the Sumatran orangutans' curiosity toward their environment would have a genetic component favored by selection over time due to separation with possibly different socio-ecological conditions (forest productivity: van Schaik et al. 2009). A similar effect of intrinsic predisposition for interest in objects was suggested for immature chimpanzees compared to the closely related bonobos (Koops et al. 2015). Further research is needed to investigate these theories and disentangle the different influences.

Is there a homologue to general intelligence in orangutans?

The psychometric findings of *g* in orangutans captured the positive correlations among test scores of important problem solving components, such as the abilities of memorizing, associative learning, spatial flexibility and causal reasoning. The core definition of general intelligence captures exactly these logical problem-solving functions, reasoning- and learning abilities. In addition, the link of *g* and curiosity emphasizes the developmental construction of general-cognitive abilities. The experiences during development biased the outcome of across task performance in orangutans, as it is expected for general intelligence in humans. Thus, *g* in orangutans is in general consistent with the content of general intelligence. However, as in humans, it has to be further investigated what the emergent property of *g* exactly represents.

We conclude that the content and structure of orangutan cognitive abilities are comparable to those of humans. The evidence for *g* in orangutans allows us to assume an evolutionary continuity in domain-general processes shared between humans and great apes. Similar processes, including socially induced curiosity (Schuppli et al. unpublished data) may have shaped general cognitive abilities and intelligence in primates over millions of years.

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General Discussion

GENERAL DISCUSSION

In this thesis, I made use of the phenotypic plasticity in a large sample of Bornean and Sumatran orangutans, our close relatives, to gain novel insights into the factors shaping the development of cognitive abilities and therefore the selective pressures favoring the evolution of intelligence. The results presented in this PhD thesis highlight an unidentified contributor that shapes intelligence in orangutans. Curiosity, which in the wild is largely absent and only elicited by social inputs, can be elicited due to special captive living conditions during youth. It significantly determined both the ability to solve novel problems and the development of domain-general cognitive abilities in orangutans. A curious response-and-exploration style presumably changes an individual's approach to its environment and therefore the quality and quantity of experiences that accumulate during development. I will first outline the main findings of all three chapters and subsequently discuss the implications of these findings.

The influences of rearing background and human contact during development on the outcome of cognitive performance were investigated in the first chapter. Orangutans that experienced contact to humans during infancy had a different orientation toward humans and expressed fundamental psychological changes concerning their problem-solving approach. The change specifically increased their motivation to explore, as represented in reduced neophobia, increased duration of exploration and a change in the nature, and thus the variety, of their exploration. As a result of their orientation toward humans, they explored the relevant parts of the apparatus more than non-curious individuals, which consequently affected their understanding of the problem-solving task, and therefore their success in solving it. It was suggested that the early exposure to humans and human artifacts in captivity produces a broader range of opportunities for learning and exploration, resulting in increased interest and innovativeness in captive apes compared to their wild conspecifics.

In my second chapter, I wanted to disentangle the causes and consequences of the phenomenon of human orientation and curiosity in orangutans to gain a better understanding of how previous individual experiences affect the developmental construction of an individual's problem-solving ability. For this purpose, I examined an individual's response-and-exploration style, its developmental construction and effects on the outcome of cognitive performance on various physical cognitive problem-solving tasks. First of all, the results show that the measurement of orientation toward humans represents a good measurement of general current curiosity in orangutans. Secondly, this curiosity was characterized by a positive response to novelty and a high motivation to explore, which, thirdly, was especially developed when individuals had experienced stable and safe living conditions, previous care by humans or social housing with conspecifics. This striking effect of curiosity was quite unexpected because orangutans are decidedly uncurious under natural conditions. Fourthly, an individual's curiosity predicted problem-solving performance very well in a variety of physical cognitive tasks, especially those in which trial-and-error facilitates finding a solution.

The third chapter investigated the underlying general abilities and its possible determinants, including curiosity and experience. Specifically, I investigated the possibility of homologues to domain-general intelligence in orangutans as has been amply demonstrated in humans through the general factor *g.* The results of this chapter indicate that my studies provide the first empirical evidence for *g* in orangutans, which is comparable to the general intelligence found in humans. The results of this study further show that curiosity is positively linked to *g*, and thus the domain-general cognitive abilities. Therefore, curiosity and the effect of experience play a crucial role in the development of higher cognitive abilities, including the domain-general processes underlying intelligence.

What makes orangutans intelligent?

When observing nonhuman animals in captive settings it is very easy to gain the impression that clever species, such as great apes, are in general very curious, inventive and prone to develop higher skills, such as tool use. This thesis clearly shows that stable captive living conditions during development, including contact with humans, significantly improved the cognitive abilities and approach to problem solving in orangutans and turned them into intelligent problem-solvers. The impression that captive nonhuman animals, especially nonhuman primates, can be notably clever and innovative is therefore not fundamentally false, but is biased and incomplete as there is plenty of evidence that under natural conditions orangutans are very neophobic and that the skill pool, critical for survival, is acquired through very different strategies, based on social learning. Therefore, orangutan intelligence did not evolve because individuals were adventurous explorers. My PhD thesis strongly emphasizes the importance of social-cultural opportunities for learning and the role of experience for the development of cognitive abilities. The innate potential for curiosity and its emancipation from social triggering in captivity tells us more about the selection pressures and mechanisms that determine intelligence in the species of orangutans and may also have important implications for how we explain the dramatic increase of intelligence in our own lineage.

Although higher cognitive abilities are costly (because they require relatively large brains), the ability to be intelligent can still be adaptively significant, as explained by the Cultural Intelligence Hypothesis. In the wild social learning is more efficient and safer than asocial learning. Therefore, once a role model is present individuals should prefer social learning. A review by Forss et al. (in review) shows this is the preference for various species, including orangutans. What is the nearly exclusive way for orangutans to gain knowledge in the wild is complemented in captivity by overall curiosity that does not need social cues to be elicited, due to lower risks and different social circumstances. Curiosity thus reflects the presence of unusual socio-cultural impact early in life and can explain why captive primates appear to be so much more intelligent than their wild counterparts (the captivity effect).

There is a dormant inherited potential of curiosity within an individual, which supports learning by increasing individual exploration once the novelty approach can be overcome through social approval. Considering the importance of social knowledge transfer in the wild these mechanisms might have evolved to ensure quick and intensive exploration once opportunities for learning are given. Therefore, general curiosity (i.e. curiosity that does not require social triggers and is directed at all aspects of the environment, including novel ones) is a by-product and its unleashing is an artifact of captivity that, once released, enables the individual to make use of its leisure in captive conditions to creatively explore, invent and become a flexible problem-solver. This is possible because the emancipation of curiosity from social triggering enables individuals in captivity to also learn in asocial situations and therefore have extended opportunities for learning. What normally is only possible in social context can now amplify on its own and bestow double opportunities for learning and gaining experience in captivity. Since social and asocial learning share similar underlying cognitive mechanisms this experience effect can quickly accumulate. As predicted by the Cultural Intelligence Hypothesis and supported by the findings of this thesis, through increased experiences an individual will develop larger skill repertoires and minds capable of better cognitive performance on a developmental, but also on an evolutionary level.

Overall, although the actual mechanisms responsible for the construction of intelligence in orangutans are of course identical in captive and wild settings (experience effect through opportunities for learning), determinants of cognitive performance and ability underlie different constraints during development in captivity than in the wild. Stable and human-enriched environments in captivity somehow catapult orangutans into becoming 'curious super-brains' with behavioral and cognitive performance highly atypical for their species under natural conditions. Consequently, the minds of the captive and wild orangutans are significantly different from each other. This difference has the following implications.

First, there may be implications for translocation and reintroduction of captive individuals into the wild (see paragraph *Implications for orangutan rehabilitation* below). Second, there is no such thing as culture-free testing of cognitive abilities, given the essential presence of social-cultural experiences on cognition during ontogeny. Previous experiences and preferences will always bias experimental testing, as already suggested by Rowe and Healy (2014). Third, to test for underlying evolutionary mechanism and selective pressures on cognition and intelligence researchers have to be aware of these differences and possibly distinguish between the two conditions. For cognitive investigations, the distinction between wild and captive orangutans is crucial. Although the possibility of unleashing the innate potential of curiosity in orangutans provides insight in the driving factors for the construction of intelligence, studies in the wild remain essential to investigate the conditions that shape the development of intelligence, and have shaped it over evolutionary time.

Implications for orangutan rehabilitation

The curiosity findings of this PhD thesis might have important implications for future orangutan rehabilitation and release into the wild. The individual's response-and-exploration style that can easily be measured through the novelty response toward unfamiliar food reveals an individual's character to deal with a novel environment. The assessment of an individual's curiosity could therefore serve to evaluate each individual's chances of successful reintroduction before it is being released.

On the one hand, individuals that are curious might be the better and more flexible learners. They theoretically should benefit from a broad pool of knowledge and inner motivation of novelty seeking that enables them to adapt more quickly to a change in environment and demands. After all, it takes a minimum of curiosity to engage with a complete new environment. Strictly non-curious or even neophobic individuals might not adapt well to a complete change in environmental conditions, as illustrated by the case of wild individuals coming to the rehabilitation stations and remaining behaviorally wild.

On the other hand, highly curious individuals, which are interested in unfamiliar humans, objects and food, might not necessarily be the ones that are best qualified for release. As I reviewed above, curiosity in the wild might have lethal consequences. There is evidence for a deadly incident of one individual that participated in my study and was released the same year. This individual had a high curious response and exploration style (within the top quartile over all measured individuals) and did not survive the first year of being free in the wild, because she was bitten by a snake. The full circumstances of this incident are not known, but it cannot be excluded that high levels of curiosity played a role in the outcome. Furthermore, a recent summary by the BOS Foundation about release success in Batikap reported that individuals that were older than 6 years of age when they arrived at the station, and thus had had more contact with humans during the sensitive period of infancy, have a higher risk of death and their success rates of release dropped by more than a half (BOS Foundation Report 2017, Table 5, p.20). This is generally in line with explanations of curiosity as shown by my study.

An additional problem is that highly curious individuals, mostly ex-pet orangutans, generally have lost their fear of humans and may enter houses after being released, thus causing trouble. Reports indicate that this scenario is very likely and a major reason why certain individuals are re-confiscated and returned to the station. It was also reported that certain individuals approach unfamiliar humans in the forest, which can also result in death.

Therefore, although it still has to be evaluated where the threshold lies for being curious enough for a successful release in a novel environment, it is highly likely that an individual's response-and-exploration style strongly affects survival in the wild upon release.

Evolution of general intelligence

This thesis has important implications for our understanding of the developmental influences that might have shaped the evolution of intelligence in primates. My results suggest evolutionary continuity of general intelligence in primates by showing the presence of domain-general cognitive abilities in orangutans, similar to the ones of humans. This supports the idea that general intelligence is a phylogenetically old phenomenon among primates. This continuity was already suggested by Deaner et al. (2006), Reader et al. (2011) and (Burkart et al. 2017). Therefore, primate 'cleverness' does not simply reflect domain-specific cognitive adaptations. As brain tissue for intelligence can be very costly, the presence of domain-general abilities in primates therefore reveals its evolutionary success. Results of this thesis confirm the predictions of the Cultural Intelligence Hypothesis (van Schaik and Burkart 2011), which describes the benefits of opportunities for social learning in overcoming environmental unpredictability and the development of bigger brains with higher intelligence in primates. Alone among primates, humans have evolved special features, such as teaching, that together with the adoption of a cooperative breeding system tremendously favored the qualitative and quantitative increase in social learning opportunities (Burkart and van Schaik 2010, van Schaik and Burkart 2011, Burkart et al. 2017). Consequently humans have evolved outstanding intelligence, which enables flexible thinking and the accumulation of great skill repertoires, including cultural repertoires.

Implications for Human Evolution

Orangutans and humans are closely related and share the same fundamental phenomena, as both are characterized by a slow life history and the presence of tolerant role models during development, which allows for maintaining high neophobia (reviewed in Forss et al. in review). The consequences of curiosity not only explain the increase of intelligence in captive great apes, but may also have important implications for how we explain the dramatic increase of intelligence and evolution of cumulative culture in our own lineage.

The conditions that facilitated the evolution of cumulative culture in hominids are the subject of intensive debate. Most commonly discussed are an increase in brain size and demographic effects, such as larger populations or more connected social networks (e.g. Henrich et al. 2016). One additional explanation for a rise in innovations is that increased curiosity due to pre-existing circumstances turned hominins into curious explorers (van Schaik et al. 2016). Modern humans are very curious, eager to seek knowledge, and show high intelligence, innovation skills and large cultural repertoires. Curiosity may serve as a link to innovation and problem-solving strategies, as it makes us seek novelty and be highly explorative, and thus not only underlies our creativity, but directly contributes to knowledge acquisition. For nonhuman animals, I have suggested that curiosity is in most cases an artifact of captivity, an environment providing for basic needs. The present findings in

orangutans therefore suggest that a major rise in innovations had to wait until our ancestors underwent the equivalent of the captivity effect and could afford to become curious explorers. The development of curiosity is especially possible in protected and safe conditions enhanced by social facilitation.

We should therefore look for indicators of such conditions during hominid evolution. One possibility is the establishment of safe home bases, protected against predators. Another is the acquisition of effective distance weapons, which turned humans into the top predator, no longer at risk from natural predators. These circumstances may have become prevalent during the Upper Paleolithic in Europe, when modern humans had become top predators, had rich food resources available as prey was easily hunted and therefore had additional time for practicing skills and experimenting with materials (van Schaik 2016). During this period cultural elements of art appeared and inventions in the field of tool manufacturing and hunting were made. In short, curiosity may have given a major, so far unappreciated boost to our ancestors' material culture that cannot be explained by brain size and demography. The rise of curiosity may therefore have strongly contributed to making humans behaviorally modern well after we became so morphologically.

Future work is needed to test this novel idea. Nonetheless, I hope this dramatic unleashing of latent cognitive potential in species that are highly conservative in the wild, shows that we should take seriously the possibility that the origin of curiosity may have served as an important non-demographic contributor to the elaboration of intelligence and culture in modern humans. I therefore conclude that curiosity might have unleashed creativity in the material culture of our ancestors.

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Supplementary Materials

SUPPLEMENTARY MATERIAL: CHAPTER 1

Orientation toward humans predicts cognitive performance in orangutans

Supplementary Table S1: Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task when excluding independent variables for the novelty response tests.

Generalized Linear Mixed Model of overall performance in the honey tool-task. Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task.				
	B	***SE***	***Z***	***p value***
Human Orientation Index	0.243	0.09	2.679	**0.007 ****
Age	-0.018	0.03	-0.582	0.561
SEX (male)	-0.619	0.53	-1.158	0.247
Species (Sumatra)	0.295	0.60	0.484	0.628
Background				
Wild vs. Rest	-0.212	0.24	-0.890	0.373
Rehab vs. Zoo	-0.131	0.30	-0.436	0.663
Unknown vs. Rehab.Rest	0.160	0.22	0.730	0.466
Human vs. Station (within rehabilitation station)	-0.489	0.52	-0.933	0.351
Mother vs. Hand (within zoo)	0.383	0.52	0.573	0.465
Accessibility (trend analysis)				
Linear	1.211	0.87	1.395	0.163
Quadratic	1.209	0.97	1.249	0.212
Cubic	0.099	0.97	0.103	0.918
Sub-task (trend analysis)				
Linear	-5.046	0.72	-6.981	**<0.001*****
Quadratic	1.512	0.42	3.567	**<0.001*****
Cubic	-0.149	0.33	-0.457	0.648
Note: Analysis included 94 individuals in 10 different zoos/rehab stations, totaling 376 observations, χ^2_{ML}= 220.60, P< 0.001				

Supplementary Table S2: Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task. Analysis without the HOI.

General Linear Mixed Model of overall performance in the honey tool-task. Parameter estimates from a binomial GLMM, predicting the probability of an animal solving the task.				
	B	***SE***	***Z***	***p value***
(Intercept)	-0.609	0.91	-0.670	0.503
Age	0.001	0.03	0.023	0.981
SEX (male)	-0.638	0.51	-1.252	0.210
Species (Sumatra)	0.186	0.56	0.332	0.740
Background				
Wild vs. Rest	-0.360	0.22	-1.604	0.109
Rehab vs. Zoo	-0.115	0.26	-0.447	0.655
Unknown vs. Rehab.Rest	0.221	0.21	1.041	0.298
Human vs. Station (within rehabilitation station)	-0.613	0.51	-1.201	0.230
Mother vs. Hand (within zoo)	0.157	0.41	0.381	0.704
Accessibility (trend analysis)				
Linear	0.910	0.81	1.118	0.263
Quadratic	1.499	0.83	1.803	0.071 .
Cubic	0.120	0.82	0.146	0.884
Sub-task (trend analysis)				
Linear	-4.905	0.66	-7.478	**<0.001 *****
Quadratic	1.509	0.39	3.830	**<0.001 *****
Cubic	0.036	0.31	0.118	0.906
Note: The model is controlling for repeated observations on each facility and individual. The performance in the honey tool-task was binary measured. The Analysis included 103 individuals in 12 different zoos/rehab stations, totaling 412 observations, $\chi^2 = 236.43$, $P < 0.001$				

Supplementary Table S3: Detailed list of all different exploration actions coded as relevant and irrelevant exploration during the time an individual engaged with the honey tool-task.

Relevant Exploration Actions	Irrelevant Exploration Actions
Insert stick into L-shaped channel	Hit (with any body parts) test apparatus or board
Insert finger into L-shaped channel	Hit (with any body parts) table on which apparatus is presented
Insert finger into I-shaped channel	Pull/ Push test apparatus, plexiglas, screws
Insert rope into I-shaped channel	Pull/ Push table or board on which apparatus is presented
Trace/ Poke finger outside glass of either I- or L-shaped channel	Touch test apparatus, plexiglas, screws (elsewhere but channels)
Trace/ Poke stick outside glass of either I- or L-shaped channel	Touch table or board on which apparatus is presented
Tool modification/ manufacture	Poke stick at apparatus, plexiglas, screws (elsewhere but channels)
Insert any other tool than stick or rope into L-shaped channel	Poke stick at board/table on which apparatus is presented
Insert any other tool than stick or rope into I-shaped channel	Touch sticks on the floor or besides test apparatus
Poke or push stick at opening of L-shaped channel	Touch ropes on the floor or besides test apparatus
Poke or push stick at opening of I-shaped channel	
Poke or push finger at opening of L-shaped channel	
Poke or push finger at opening of I-shaped channel	

Supplementary Table S4: Linear Mixed-Effects Model of relevant exploration variety controlling for repeated observations on each facility.

	B	*SE*	*df*	*t value*	*p value*
(Intercept)	1.209	1.41	48.66	0.857	0.396
HOI	0.221	0.05	80.07	4.049	**<0.001 *****
Age	0.014	0.03	80.84	0.414	0.680
SEX (male)	-0.059	0.55	79.52	-0.106	0.916
Species (Sumatra)	0.946	0.87	6.31	1.084	0.318
Background					
Wild vs. Rest	0.162	0.25	75.37	0.652	0.517
Rehab vs. Zoo	0.356	0.33	42.06	1.063	0.294
Unknown vs. Rehab.Rest	0.408	0.23	80.76	1.746	0.085 .
Human vs. Station (within rehabilitation station)	-0.257	0.53	79.81	-0.483	0.630
Mother vs. Hand (within zoo)	0.314	0.58	65.78	0.544	0.589
Accessibility (trend analysis)					
Linear	0.316	1.11	12.64	0.285	0.780
Quadratic	0.467	1.13	23.52	0.411	0.685
Cubic	1.540	1.04	77.21	1.486	0.141

Note: The model is controlling for repeated observations on each facility. The analysis was totaling 94 observations in 10 different zoos/rehab stations, $\chi^2 = 30.91$, $p < .0005$

Supplementary Table S5: Pairwise comparisons of the Human Orientation Index (HOI) between the different background and rearing categories.

Pairwise comparisons of HOI between different background categories, controlling for age, sex, island and repeated observations from each zoo and rehabilitation station.				
	B	***SE***	***Z***	***p value***
Hand-reared zoo - Station	1.649	2.03	0.814	0.960
Human - Station	-1.452	1.35	-1.078	0.877
Mother-reared zoo - Station	-0.605	1.62	-0.372	0.999
Unknown - Station	-0.279	1.28	-0.217	1.000
Wild - Station	-3.568	2.46	-1.450	0.670
Human – Hand-reared zoo	-3.102	1.82	-1.707	0.497
Mother-reared zoo – Hand-reared zoo	-2.254	1.50	-1.499	0.637
Unknown – Hand-reared zoo	-1.928	1.74	-1.106	0.864
Wild – Hand-reared zoo	-5.217	2.70	-1.931	0.354
Mother-reared zoo - Human	0.847	1.35	0.626	0.987
Unknown - Human	1.174	0.94	1.249	0.792
Wild - Human	-2.116	2.25	-0.941	0.927
Unknown – Mother-reared zoo	0.326	1.25	0.260	1.000
Wild – Mother-reared zoo	-2.963	2.41	-1.227	0.805
Wild - Unknown	-3.289	2.41	-1.468	0.658
P-values corrected for multiple comparisons using Tukey.				

Supplementary Table S6 study subjects.

Individual	Age in years at testing	years in captivity	species	current housing	Category
Amin	6	0.5	*Pongo abelii*	Reha-Station	unknown background
Amos	13	13.0	*Pongo pygmaeus*	Zoo	Mother reared
Andalas	3	0.5	*Pongo abelii*	Reha-Station	unknown background
Anette	30	30.0	*Pongo abelii*	Zoo	Mother reared
Ari	10	8.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Ayu	6	0.5	*Pongo abelii*	Reha-Station	unknown background
Bahruni	10	0.5	*Pongo abelii*	Reha-Station	wild/ translocated
Bambang	10.5	5.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Batu	14	14.0	*Pongo pygmaeus*	Zoo	Mother reared
Bella	14.5	10.0	*Pongo pygmaeus*	Reha-Station	unknown background
Binti	13	13.0	*Pongo pygmaeus*	Zoo	Human hand reared
Budi	8	8.0	*Pongo abelii*	Zoo	Mother reared
Cane	10	0.0	*Pongo abelii*	Reha-Station	wild/ translocated
Cantik	10	8.0	*Pongo pygmaeus*	Reha-Station	unknown background
Ceky Chan	6	0.0	*Pongo abelii*	Reha-Station	Background with humans
Cherie	18	18.0	*Pongo pygmaeus*	Zoo	Mother reared
Cici	15	10.0	*Pongo pygmaeus*	Reha-Station	unknown background
Dagu	28	28.0	*Pongo abelii*	Zoo	Mother reared
Dana	25	25.0	*Pongo abelii*	Zoo	Mother reared
Dandim	12	7.0	*Pongo pygmaeus*	Reha-Station	unknown background
Dewa	12	10.0	*Pongo pygmaeus*	Reha-Station	unknown background
Djamuna	13	13.0	*Pongo abelii*	Zoo	Mother reared
Dokana	25	25.0	*Pongo abelii*	Zoo	Mother reared
Dora	3.5	2.0	*Pongo abelii*	Reha-Station	Background with humans
Duanne	10	8.0	*Pongo pygmaeus*	Reha-Station	unknown background
Edwin	11.5	7.0	*Pongo pygmaeus*	Reha-Station	unknown background
Embrie	10	8.0	*Pongo pygmaeus*	Reha-Station	unknown background
Franky	7	0.5	*Pongo abelii*	Reha-Station	unknown background
Friend	5.5	3.5	*Pongo abelii*	Reha-Station	unknown background
Gagak	9.5	8.0	*Pongo pygmaeus*	Reha-Station	Reha-Station reared
Galih	10	7.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Gambira	18	18.0	*Pongo pygmaeus*	Zoo	Mother reared
Gina	49	45.0	*Pongo abelii*	Zoo	Mother reared
Gober	25	5.0	*Pongo abelii*	Reha-Station	wild/ translocated
Harry	8.5	7.0	*Pongo pygmaeus*	Reha-Station	Reha-Station reared
Hulu	14	8.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Imas	9.5	8.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Inou	17	15.0	*Pongo pygmaeus*	Reha-Station	unknown background
Ito	6	6.0	*Pongo pygmaeus*	Zoo	Mother reared
Jack2	9	6.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Jacky	5	1.0	*Pongo abelii*	Reha-Station	Background with humans
Janu	6	4.0	*Pongo pygmaeus*	Reha-Station	unknown background
Jarot	5	4.0	*Pongo abelii*	Reha-Station	Reha-Station reared
Jarwo	15	10.0	*Pongo pygmaeus*	Reha-Station	unknown background
Jaya	9	9.0	*Pongo abelii*	Zoo	Mother reared
Jill	8	7.0	*Pongo pygmaeus*	Reha-Station	Reha-Station reared
Jose	21	21.0	*Pongo pygmaeus*	Zoo	Mother reared
Julius	5	2.0	*Pongo abelii*	Reha-Station	Background with humans
Karan	10	8.0	*Pongo pygmaeus*	Reha-Station	unknown background
Karen	15	9.0	*Pongo pygmaeus*	Reha-Station	unknown background

Kasmin	10.5	9.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Kevin	32	32.0	*Pongo pygmaeus*	Zoo	Human hand reared
Kibriah	36	36.0	*Pongo pygmaeus*	Zoo	Human hand reared
Kila	13	13.0	*Pongo abelii*	Zoo	Mother reared
King	17	10.0	*Pongo pygmaeus*	Reha-Station	unknown background
Kraba	12	10.0	*Pongo pygmaeus*	Reha-Station	unknown background
Lanang	11	10.0	*Pongo pygmaeus*	Reha-Station	Reha-Station reared
Mali	20	20.0	*Pongo pygmaeus*	Zoo	Mother reared
Mandi	14	14.0	*Pongo pygmaeus*	Zoo	Human hand reared
Mawoto	17	13.0	*Pongo pygmaeus*	Reha-Station	unknown background
Maya	5	5.0	*Pongo abelii*	Zoo	Mother reared
MercedeS	12	10.0	*Pongo pygmaeus*	Reha-Station	unknown background
Natalia	18	0.0	*Pongo abelii*	Reha-Station	wild/ translocated
Natalie	11	9.0	*Pongo pygmaeus*	Reha-Station	unknown background
Niken	16	14.0	*Pongo pygmaeus*	Reha-Station	unknown background
Nonja	36	36.0	*Pongo pygmaeus*	Zoo	Human hand reared
Oracle	8.5	7.0	*Pongo pygmaeus*	Reha-Station	Reha-Station reared
Otong	13	11.0	*Pongo pygmaeus*	Reha-Station	unknown background
Padana	16	16.0	*Pongo abelii*	Zoo	Mother reared
Pilar	11	9.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Pini	25	25.0	*Pongo abelii*	Zoo	Mother reared
Pongo	15	15.0	*Pongo pygmaeus*	Zoo	Mother reared
Radja	52	51.0	*Pongo pygmaeus*	Zoo	Mother reared
Raja	13	13.0	*Pongo abelii*	Zoo	Mother reared
Ramon	18	18.0	*Pongo pygmaeus*	Zoo	Human hand reared
Roma	17	13.0	*Pongo pygmaeus*	Reha-Station	unknown background
Rowland	10	8.0	*Pongo pygmaeus*	Reha-Station	unknown background
Runtu	13	8.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Sabin	9.5	9.0	*Pongo pygmaeus*	Reha-Station	Reha-Station reared
Sandakan	32	32.0	*Pongo pygmaeus*	Zoo	Mother reared
Sari	43	43.0	*Pongo pygmaeus*	Zoo	Human hand reared
Sarimin	11	9.0	*Pongo pygmaeus*	Reha-Station	unknown background
Silvia	49	48.0	*Pongo pygmaeus*	Zoo	Mother reared
Sony	16	12.0	*Pongo pygmaeus*	Reha-Station	unknown background
Suaq	5	5.0	*Pongo abelii*	Zoo	Mother reared
Sule	7	4.0	*Pongo pygmaeus*	Reha-Station	unknown background
Summer	13	13.0	*Pongo pygmaeus*	Zoo	Mother reared
Suri	5	3.0	*Pongo abelii*	Reha-Station	Background with humans
Tanah	5	5.0	*Pongo abelii*	Zoo	Mother reared
Tao	8	8.0	*Pongo abelii*	Zoo	Mother reared
Temmy	31	31.0	*Pongo pygmaeus*	Zoo	Human hand reared
Toba	18	18.0	*Pongo abelii*	Zoo	Mother reared
Trio	16	13.0	*Pongo pygmaeus*	Reha-Station	unknown background
Ulin	14	11.0	*Pongo pygmaeus*	Reha-Station	unknown background
Vendel	13	13.0	*Pongo abelii*	Zoo	Mother reared
Victor	10.5	9.0	*Pongo pygmaeus*	Reha-Station	Background with humans
Victoria	31	31.0	*Pongo pygmaeus*	Zoo	Human hand reared
Walter	23	23.0	*Pongo abelii*	Zoo	Mother reared
Wattana	18	18.0	*Pongo pygmaeus*	Zoo	Human hand reared
Willy	6	3.0	*Pongo abelii*	Reha-Station	Background with humans
Winda	12	7.0	*Pongo pygmaeus*	Reha-Station	wild/ translocated
Yogi	8	8.0	*Pongo pygmaeus*	Reha-Station	Reha-Station reared
Zatarra	10	8.0	*Pongo pygmaeus*	Reha-Station	unknown background

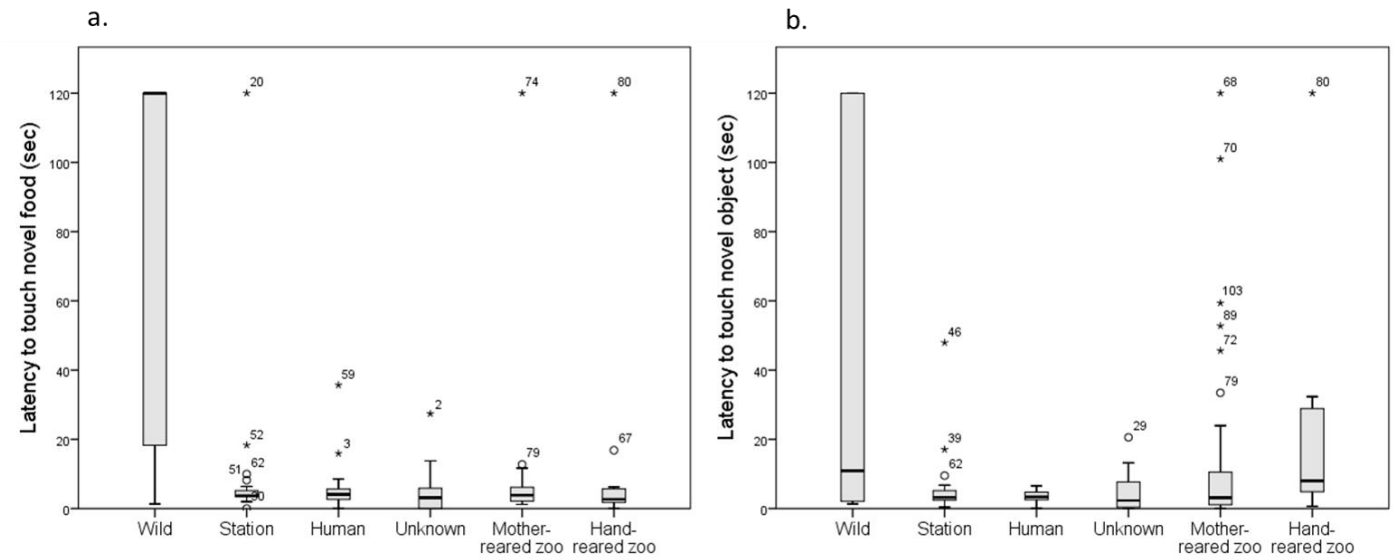


Figure S1: Novelty response across individuals of different background categories. (**a**) Latency to touch novel food and (**b**) Latency to touch a novel object.

SUPPLEMENTARY MATERIAL: CHAPTER 2

Curiosity boosts orangutan problem-solving ability

The human orientation index (HOI)

The human orientation test was composed of four consecutive conditions (30 s each) and lasted for 2 min. In the first condition the unfamiliar man approached the enclosure and positioned himself in front (1 m to the bars/mesh) where the subject was located. For the first 30 s, he stood still with his body oriented sideways (laterally) to the subject. In the second condition the man turned around to directly face the orang-utan. Then he tried to establish eye contact with the individual. In the third condition the man took some familiar food (peanuts) out of his pocket and held it in his hand in front of his body, well visible but out of reach to the orang-utan. In the fourth condition the man offered the food out of reach to the orang-utan.

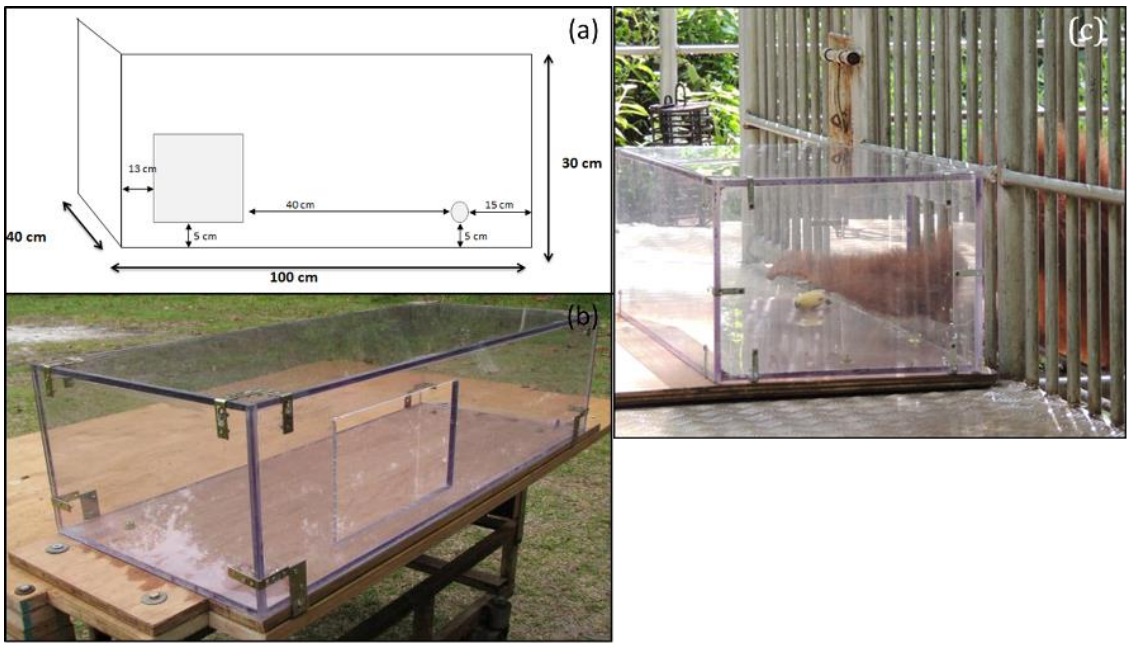
Importantly, no other human was present during testing and the test was recorded on video. From the video the first reaction of the orang-utan and its proximity to the man for the first 2 s of first sight were coded for each condition. We scored the first behavioural reaction of the orang-utan as follows: 0= a negative reaction, such as retreat, stress vocalization, piloerection, nervous swinging or turning away from the human; 1= a neutral reaction, defined as resting, moving calmly or play behaviour; 2= a positive reaction, if the orang-utan approached the human; and 3= an actively positive reaction, if the orang-utan begged (either by using lips or hands), tried in any other active way to contact the human or attempted to trade objects from the enclosure for food.

In addition, we scored the orang-utan's proximity to the man in the following way: 0= the orang-utan positioned itself as far as possible from the human; 1= the orang-utan was further than 1 m from the human; 2= the orang-utan was within 1 m from the human; and 3= the orang-utan was directly at the bars/mesh and positioned itself as close as possible to the human.

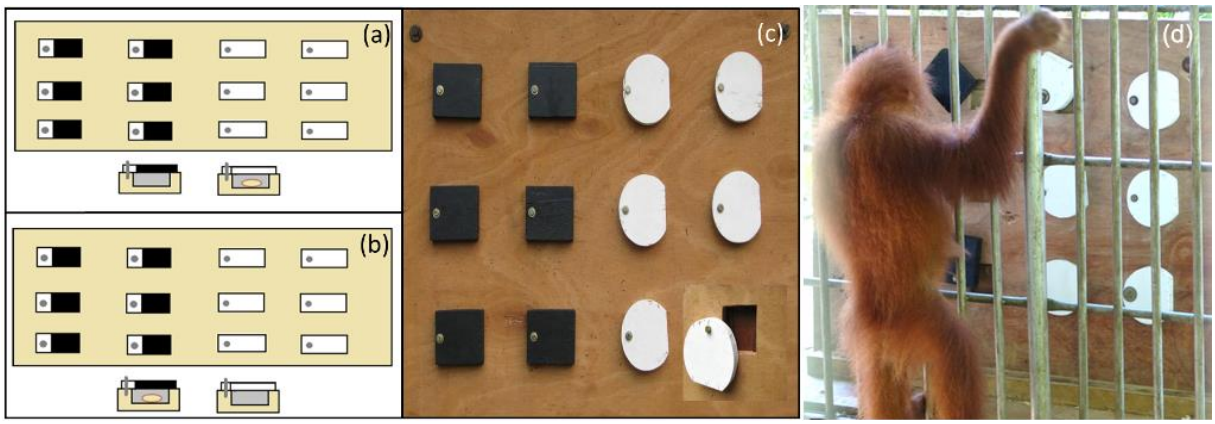
To ensure we recorded any possible substantial interest in humans when the surprise had waned, we also scored whether any active contact behaviour occurred during the 30 s of each condition. Thus, in total the HOI consisted of the summed first reactions of an individual towards an unfamiliar man, in addition to the proximity to him, with the eventual score ranging from zero to 28.

Supplementary Figures

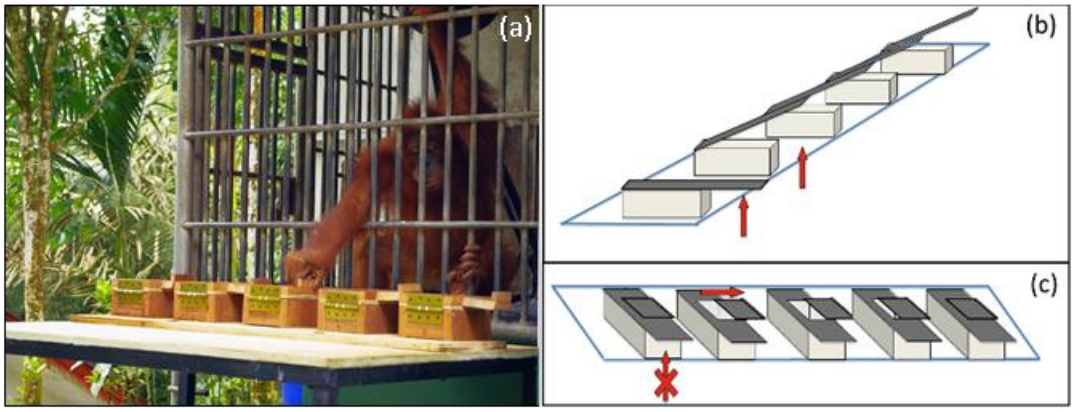
Supplementary Figure S1: Presentation table (140 x 100 cm and 110–160 cm high; the table was adjustable in height) for elevated enclosures. (a) The presentation table with an additional board (180 x 120 cm and 3 cm deep) for experiments that required a vertical position. (b) The table presented during the Box Task. The individual reached through the bars to get access to the apparatus.



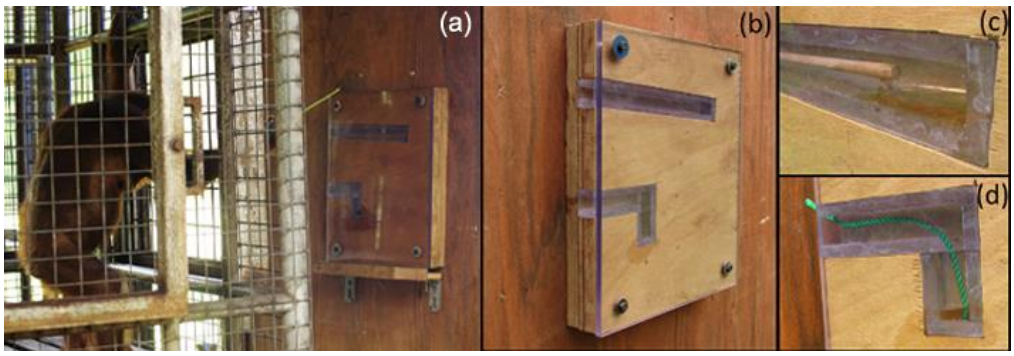
Supplementary Figure S2: Detour Reaching. (a) A schematic view including technical measurements of the apparatus used for Detour Reaching. The box (100 x 30 cm and 40 cm high) had a small hole (diameter 2 cm) on the front on the right and a large hole (29 cm and 19 cm high) on the left. (b) The Detour Reaching box was screwed onto the presentation table and could be presented from the outside of the cage. (c) Sumatran orang-utan solving the task by reaching for the bait, a banana, through the big hole on the left.



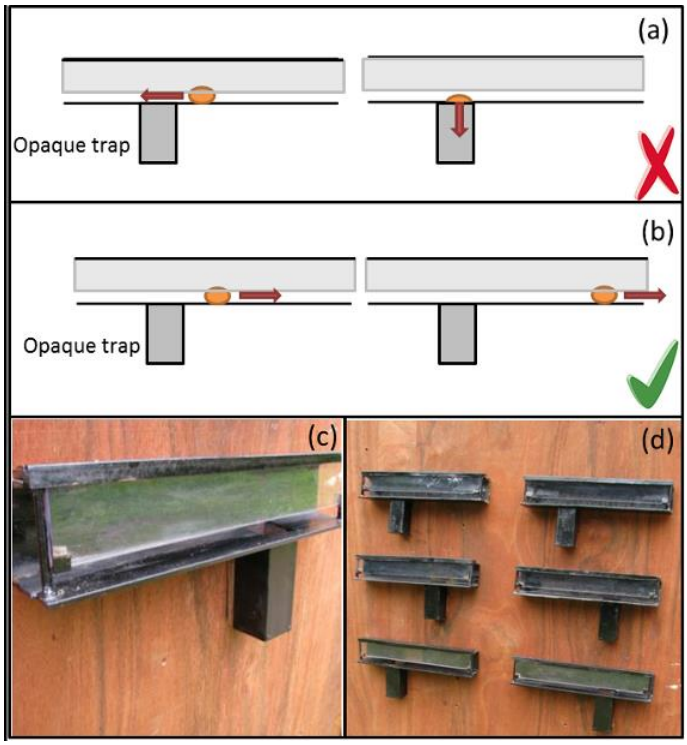
Supplementary Figure S3: Reversal Learning with 12 doors (13 × 10 cm, 15 cm apart). (a) Schematic view of the learning phase of the Reversal Learning. The subject learned the association of food and location (here: right). The association with location was enhanced with colours (here: white). (b) Schematic view of the Reversal Phase. The old association (right, white) no longer held and the association 'left, black' had to be learned. (c) The Reversal Learning board as it was presented to the individual. (d) Sumatran subject conducting the Reversal Learning task by reaching through the bars and turning the doors.



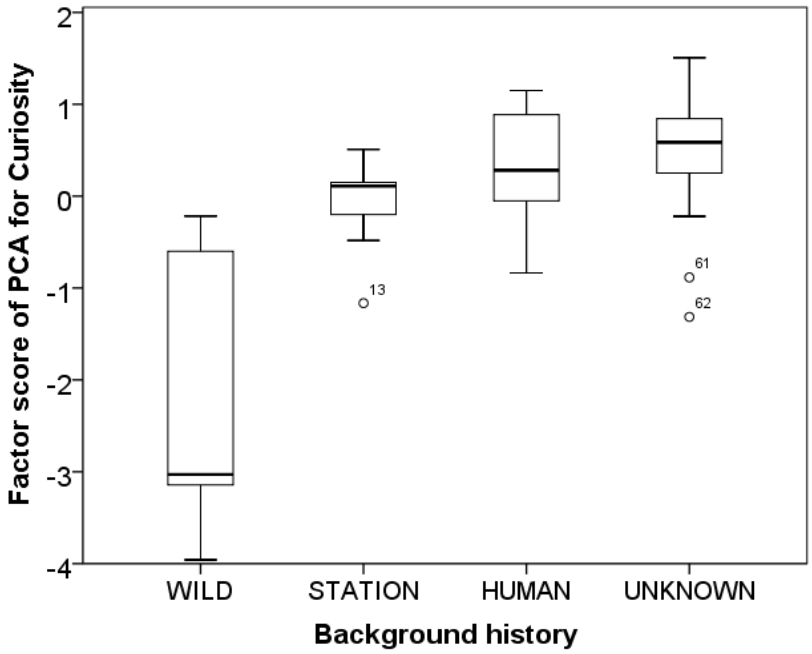
Supplementary Figure S4: Box Task with five wooden boxes (20 x 15 cm and 8 cm high). (a) Sumatran orang-utan conducting the box task, here using the sliding doors during its second presentation. (b) First presentation of the apparatus. The lid could be flipped open. (c) Second presentation of the apparatus. Doors could be slid open to retrieve the food reward.



Supplementary Figure S5: Visible Honey Tool Trap. (a) Bornean individual using the stick on the Honey Tool apparatus. (b) Wooden box (80 x 50 cm and 7 cm deep) with two embedded transparent Makrolon tubes: a straight channel (30 x 5 cm and 5 cm deep) and a curved L-shaped channel [15 cm long (10 cm with an additional 5 cm bend), 5 cm wide and 5 cm deep]. (c) Stick inserted in the straight channel to obtain honey (correct solution). (d) Rope inserted in the curved channel to obtain honey (correct solution).



Supplementary Figure S6: Tube Task with six tubes (37 x 6 cm and 7.5 cm high). Subjects could use their fingers to reach through the slot and to slide the bait along the tube. (a) Wrong direction to slide the bait. Bait falls into the opaque trap. (b) Correct direction to slide the bait. Bait can be retrieved out of the tube. (c) Single tube, made of metal with a transparent Makrolon plate so the subject could see the bait and run a finger through the slot. (d) Complete test design: six tubes on a vertical board.



Supplementary Figure S7: Box plots of the curiosity scores over the different background categories. The box represents observations inside the 25–75 percentile range, whiskers indicate the minimum to the maximum datum within 1.5 times the interquartile range, the internal box line is the median and circles with numbers of individuals represent outlying data points.

Supplementary Tables

Supplementary Table S1: Overview of study subjects

Individual	Age (years)	Sex	Species	Background
Amin	6	Male	*Pongo abelii*	Unknown
Andalas	3	Female	*Pongo abelii*	Unknown
Ari	10	Male	*Pongo pygmaeus*	Human
Ayu	6	Female	*Pongo abelii*	Unknown
Bahruni	10	Male	*Pongo abelii*	Wild
Bambang	10.5	Male	*Pongo pygmaeus*	Human
Bella	14.5	Female	*Pongo pygmaeus*	Unknown
Cane	10	Male	*Pongo abelii*	Wild
Cantik	10	Female	*Pongo pygmaeus*	Unknown
Ceky Chan	6	Male	*Pongo abelii*	Human
Cici	15	Female	*Pongo pygmaeus*	Unknown
Dandim	12	Male	*Pongo pygmaeus*	Unknown
Dewa	12	Male	*Pongo pygmaeus*	Unknown
Dora	3.5	Female	*Pongo abelii*	Human
Duanne	10	Male	*Pongo pygmaeus*	Unknown
Edwin	11.5	Male	*Pongo pygmaeus*	Unknown
Embrie	10	Female	*Pongo pygmaeus*	Unknown
Franky	7	Male	*Pongo abelii*	Unknown
Friend	5.5	Male	*Pongo abelii*	Unknown
Gagak	9.5	Male	*Pongo pygmaeus*	Station
Galih	10	Male	*Pongo pygmaeus*	Human
Gober	25	Female	*Pongo abelii*	Wild
Harry	8.5	Male	*Pongo pygmaeus*	Station
Hulu	14	Male	*Pongo pygmaeus*	Human
Imas	9.5	Female	*Pongo pygmaeus*	Human
Inou	17	Male	*Pongo pygmaeus*	Unknown
Jack2	9	Male	*Pongo pygmaeus*	Human
Jacky	5	Female	*Pongo abelii*	Human
Jarot	5	Male	*Pongo abelii*	Station
Jarwo	15	Male	*Pongo pygmaeus*	Unknown
Jill	8	Male	*Pongo pygmaeus*	Station
Julius	5	Male	*Pongo abelii*	Human
Karan	10	Female	*Pongo pygmaeus*	Unknown
Karen	15	Female	*Pongo pygmaeus*	Unknown
Kasmin	10.5	Female	*Pongo pygmaeus*	Human
King	17	Male	*Pongo pygmaeus*	Unknown
Kraba	12	Female	*Pongo pygmaeus*	Unknown
Lanang	11	Male	*Pongo pygmaeus*	Station

Mawoto	17	Male	*Pongo pygmaeus*	Unknown
MercedeS	12	Female	*Pongo pygmaeus*	Unknown
Natalia	18	Female	*Pongo abelii*	Wild
Natalie	11	Female	*Pongo pygmaeus*	Unknown
Niken	16	Female	*Pongo pygmaeus*	Unknown
Oracle	8.5	Male	*Pongo pygmaeus*	Station
Otong	13	Male	*Pongo pygmaeus*	Unknown
Pilar	11	Female	*Pongo pygmaeus*	Human
Roma	17	Female	*Pongo pygmaeus*	Unknown
Rowland	10	Male	*Pongo pygmaeus*	Unknown
Runtu	13	Female	*Pongo pygmaeus*	Human
Sabin	9.5	Male	*Pongo pygmaeus*	Station
Sarimin	11	Male	*Pongo pygmaeus*	Unknown
Sony	16	Male	*Pongo pygmaeus*	Unknown
Sule	7	Female	*Pongo pygmaeus*	Unknown
Suri	5	Female	*Pongo abelii*	Human
Trio	16	Male	*Pongo pygmaeus*	Unknown
Ulin	14	Female	*Pongo pygmaeus*	Unknown
Victor	10.5	Male	*Pongo pygmaeus*	Human
Willy	6	Female	*Pongo abelii*	Human
Winda	12	Female	*Pongo pygmaeus*	Wild
Yogi	8	Male	*Pongo pygmaeus*	Station
Zatarra	10	Male	*Pongo pygmaeus*	Unknown

Supplementary Table S2: Parameter estimates and associated standard errors, obtained from a linear mixed-effects model of PC 1 'curiosity' over 16 'Human' background individuals

	Estimate	SE	*df*	*t*	*P*
(Intercept)	-0.477	0.279	5.30	-1.711	0.145
Age on arrival at station	0.224	0.062	13.96	3.633	**0.003**

The model controls for repeated observations at each rehabilitation station (random effect). $N_{observations}$ = 16, $N_{stations}$ = 3, χ^2= 10.70, *P*= 0.001. Significant *P* value is shown in bold.

SUPPLEMENTARY MATERIAL: CHAPTER 3

General Cognitive Abilities in Orangutans (*Pongo abelii and Pongo pygmaeus*)

Supplementary Figures please see p. 134

Supplementary Tables

Supplementary Table S1: study subjects

Individual	Sex	Age (years)	Species	Background Category	Data set
Amin	male	6	*Pongo abelii*	unknown	conservative
Andalas	female	3	*Pongo abelii*	unknown	conservative
Ari	male	10	*Pongo pygmaeus*	human	conservative
Ayu	female	6	*Pongo abelii*	unknown	conservative
Bahruni	male	10	*Pongo abelii*	wild	conservative
Bambang	male	10.5	*Pongo pygmaeus*	human	conservative
Bella	female	14.5	*Pongo pygmaeus*	unknown	conservative
Cantik	female	10	*Pongo pygmaeus*	unknown	conservative
Ceky Chan	male	6	*Pongo abelii*	human	conservative
Cici	female	15	*Pongo pygmaeus*	unknown	conservative
Dewa	male	12	*Pongo pygmaeus*	unknown	conservative
Dora	female	3.5	*Pongo abelii*	human	conservative
Duanne	male	10	*Pongo pygmaeus*	unknown	conservative
Edwin	male	11.5	*Pongo pygmaeus*	unknown	conservative
Embrie	female	10	*Pongo pygmaeus*	unknown	conservative
Franky	male	7	*Pongo abelii*	unknown	conservative
Friend	male	5.5	*Pongo abelii*	unknown	conservative
Galih	male	10	*Pongo pygmaeus*	human	conservative
Harry	male	8.5	*Pongo pygmaeus*	station	conservative
Hulu	male	14	*Pongo pygmaeus*	human	conservative
Imas	female	9.5	*Pongo pygmaeus*	human	conservative
Jack2	male	9	*Pongo pygmaeus*	human	conservative
Jacky	female	5	*Pongo abelii*	human	conservative
Janu	male	6	*Pongo pygmaeus*	unknown	conservative
Jarot	male	5	*Pongo abelii*	station	conservative
Jill	male	8	*Pongo pygmaeus*	station	conservative
Julius	male	5	*Pongo abelii*	human	conservative
Karan	female	10	*Pongo pygmaeus*	unknown	conservative
Karen	female	15	*Pongo pygmaeus*	unknown	conservative
King	male	17	*Pongo pygmaeus*	unknown	conservative
Kraba	female	12	*Pongo pygmaeus*	unknown	conservative
Lanang	male	11	*Pongo pygmaeus*	station	conservative
Mawoto	male	17	*Pongo pygmaeus*	unknown	conservative
Mercedes	female	12	*Pongo pygmaeus*	unknown	conservative
Natalie	female	11	*Pongo pygmaeus*	unknown	conservative
Niken	female	16	*Pongo pygmaeus*	unknown	conservative
Oracle	male	8.5	*Pongo pygmaeus*	station	conservative

Otong	male	13	*Pongo pygmaeus*	unknown	conservative
Pilar	female	11	*Pongo pygmaeus*	human	conservative
Roma	female	17	*Pongo pygmaeus*	unknown	conservative
Rowland	male	10	*Pongo pygmaeus*	unknown	conservative
Runtu	female	13	*Pongo pygmaeus*	human	conservative
Sabin	male	9.5	*Pongo pygmaeus*	station	conservative
Sarimin	male	11	*Pongo pygmaeus*	unknown	conservative
Sule	female	7	*Pongo pygmaeus*	unknown	conservative
Suri	female	5	*Pongo abelii*	human	conservative
Trio	male	16	*Pongo pygmaeus*	unknown	conservative
Ulin	female	14	*Pongo pygmaeus*	unknown	conservative
Victor	male	10.5	*Pongo pygmaeus*	human	conservative
Willy	female	6	*Pongo abelii*	human	conservative
Winda	female	12	*Pongo pygmaeus*	wild	conservative
Yogi	male	8	*Pongo pygmaeus*	station	conservative
Zatarra	male	10	*Pongo pygmaeus*	unknown	conservative
Gagak	male	9.5	*Pongo pygmaeus*	station	extended (imputed Box Task)
Kasmin	female	10.5	*Pongo pygmaeus*	human	extended (imputed Box Task)
Natalia	female	18	*Pongo abelii*	wild	extended (imputed Box Task)
Inou	male	17	*Pongo pygmaeus*	unknown	extended (imputed Detour Reaching)

Ranked dataset with 53 individuals

Supplementary Table S2: Description of tasks and measurements with ranks applied

Cognitive ability	Task	Measurement	Median (min/max)	N
Rank Flexibility	Box Task	Number of boxes opened; largest rank describes best performance (5 boxes) and smallest worst performance (0 boxes)	27.5 (2.5/45.5)	53
Rank Inhibitory Control	Detour Reaching	Latency to first explore non-food side (show inhibit behaviour); largest rank describes best performance (small latency) and smallest worst performance (no inhibition)	27 (3/51)	53
Rank Tool use	Honey Tool Trap	Guttman scale of goal directed tool use; largest rank describes best performance (successfully fishing honey) and smallest worst performance (random exploration)	30 (3.5/48.5)	53
Rank Learning Remembering Reversal Learning	Reversal Learning	Scale of learned, remembered, reversal learned; largest rank describes best performance (successfully reversal learning) and smallest worst performance (no learning, therefor no memory and no reversal learning)	25 (4/42.5)	53
Rank Causal Reasoning	Tube Trap Task	Number rewards retrieved in all three trials; largest rank describes best performance (highest number of rewards) and smallest worst performance (no reward obtained)	27.5 (1.5/52.5)	53

Conservative data set with 53 individuals

Supplementary Table S3:
Spearman-Rho correlation matrix of the five cognitive domains of the problem-solving tasks (*N=53*)

	Flexibility	**Inhibitory Control**	**Tool use**	**Learning Remembering Reversal Learning**	**Causal Reasoning**
Flexibility	-	.027	.099	.247	.060
Inhibitory Control		-	.080	.116	.076
Tool use			-	-.028	.114
Learning Remembering Reversal Learning				-	.333

Note: Bonferroni niveau of significance p< .01 (α/N=.05/5)

Extended data set with 57 individuals

Supplementary Table S4: Principal Component Matrix of the five problem-solving domains, N=57 (imputed data set)

Item	Loadings	
	g	***Ability of Tool use***
% of variance	32.12	22.58
Eigenvalues	1.61	1.13
Learning & Remembering & Reversal Learning	**.743**	-.412
Causal Reasoning	**.679**	-.201
Flexibility	**.500**	-.069
Inhibitory Control	**.525**	**.505**
Tool use	.261	**.812**

Note: N = 53, Rotation = none.

Loadings > .50 appear in bold

Ranked dataset with 53 individuals

Supplementary Table S5: Principal Component Matrix of the five problem-solving domains on the ranked dataset

Item	Item Loadings	
	g	***Ability of Tool use***
% of variance	30.14	20.73
Eigenvalues	1.51	1.04
Rank Learning & Remembering & Reversal Learning	**.765**	-.376
Rank Causal Reasoning	**.676**	-.065
Rank Flexibility	**.524**	-.079
Rank Inhibitory Control	.346	.438
Rank Tool use	.267	**.832**

Note: N = 53, Rotation = none.

Loadings > .50 and <-.50 appear in bold

Explorative Factor Analysis with 53 individuals

Supplementary Table S6 Exploratory Factor Analysis (Maximum-Likelihood) of the five problem-solving domains

Item	Factor Loadings
	g
% of variance	22.51
Eigenvalues	1.12
Learning & Remembering & Reversal Learning	**.687**
Causal Reasoning	**.584**
Flexibility	.407
Inhibitory Control	.333
Tool use	.191

Note: N = 53, Rotation = none.

Factor loadings > .50 appear in bold

Conservative data set with 53 individuals

Supplementary Table S7 (Health instead of Age): Linear Model of variable *g* (N=53)

	Estimate	***Std. Error***	***Pr(>|z|)***
(Intercept)	0.124	0.27	0.645
Health (yes)	-0.029	0.42	0.946
Sex (male)	-0.033	0.27	0.904
Background			
Wild vs. others	-0.046	0.17	0.790
others vs. Unknown	-0.045	0.10	0.663
Station vs. Human	0.088	0.23	0.706
Rehabilitation Station			
Sumatra vs. Borneo	0.191	0.10	0.074
Borneo 1 vs. Borneo 2	-0.476	0.17	**0.007****

Note: F-statistic: 2.236 on 7 and 45 DF, p-value <.05

Dataset with 53 individuals and LEARNING as a separate variable

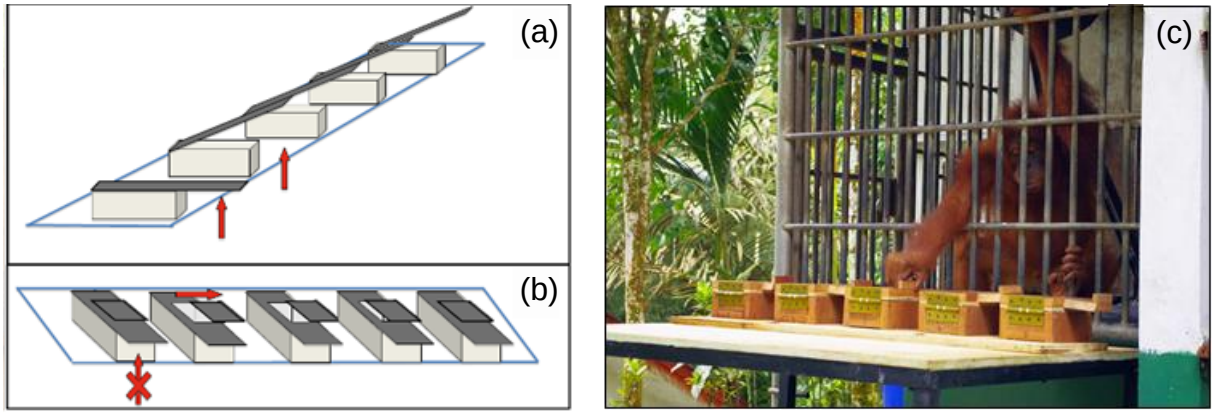
Supplementary Table S8: Principal Component Matrix of the five problem-solving domains with Learning included as a separate variable

Item	Loadings	
	g	***Ability of Tool use***
% of variance	34.39	18.38
Eigenvalues	2.06	1.10
Learning & Remembering & Reversal Learning	**.872**	-.226
Learning	**.831**	-.225
Causal Reasoning	**.581**	.062
Flexibility	.409	.064
Inhibitory Control	.258	**.654**
Tool use	.203	**.752**

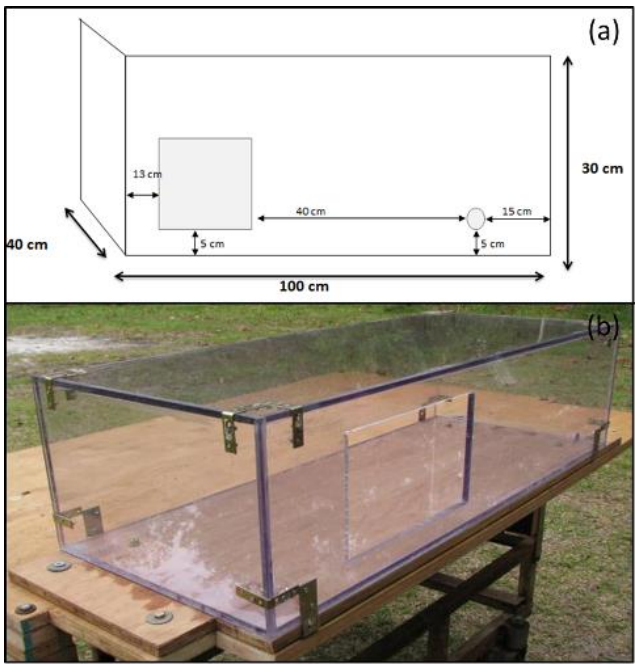
Note: N = 53, Rotation = none.

Loadings > .50 appear in bold

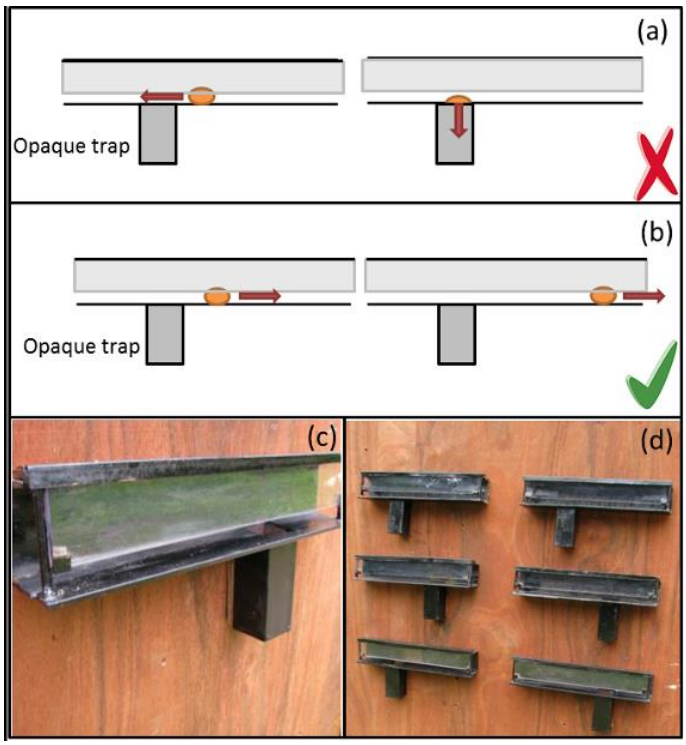
Supplementary Fig. S1: Presentation table (L 140 cm x W 100 cm x H 110 – 160 cm adjustable in height) for elevated enclosures. a) The presentation table with an additional board (L 180 cm x W 120 cm x D 3 cm) for experiments that require a vertical position. b) The table during testing of the Box Task. The individuals had access to the apparatus by reaching through the bars.



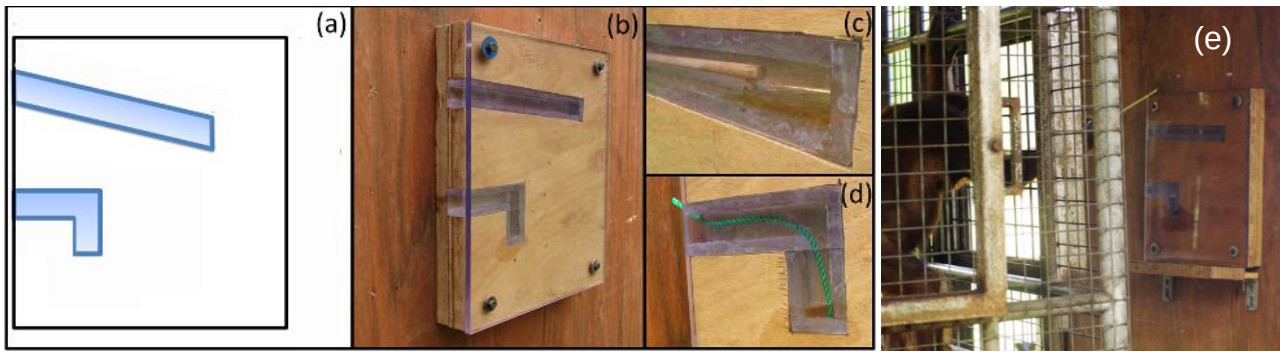
Supplementary Fig. S2: Box-Task with five wooden boxes (L 20 cm x W 15 cm x H 8 cm). (a) Schematic view of 1st presentation of the apparatus. Lid can be flipped open. (b) 2nd presentation of the apparatus. Sliding doors can be opened in order to retrieve food reward. (c) Sumatran orangutan conducting the box task, here using the sliding doors during the 2nd presentation.



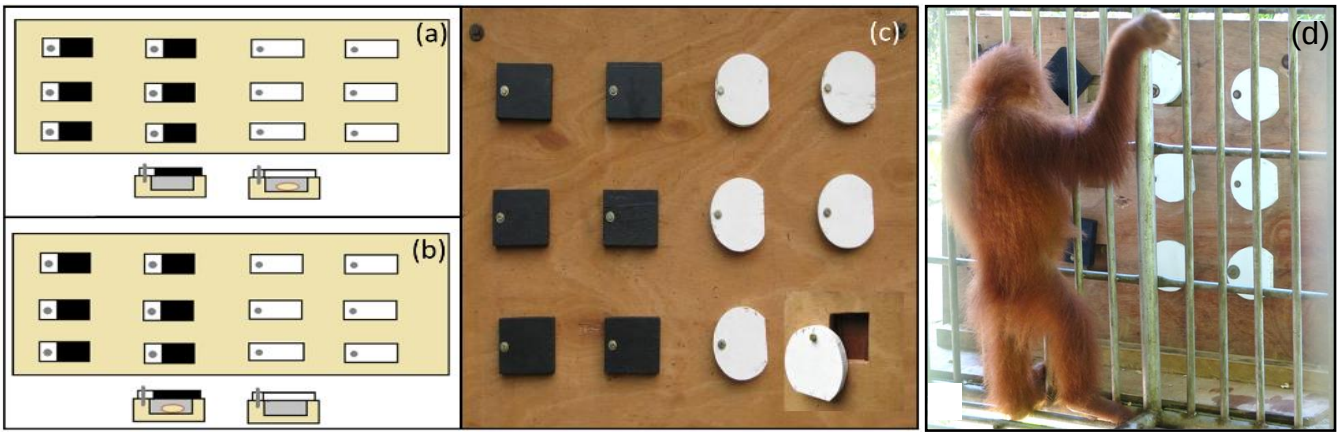
Supplementary Fig. S3: Detour Reaching. a) A schematic view including technical measurements of the apparatus used for Detour Reaching: Box (L 100 cm x W 30 cm x H 40 cm) that has two openings at the front side, one small hole (∅ 2 cm) at the right front and one large opening (L 29 cm x H 19 cm) at the left front of the box,. b) Detour Reaching Box is screwed on the presentation table and can be presented from outside of the cage. c) Sumatran orangutan solving the task by reaching for the bait, a banana, through the big hole on the left front of the box.



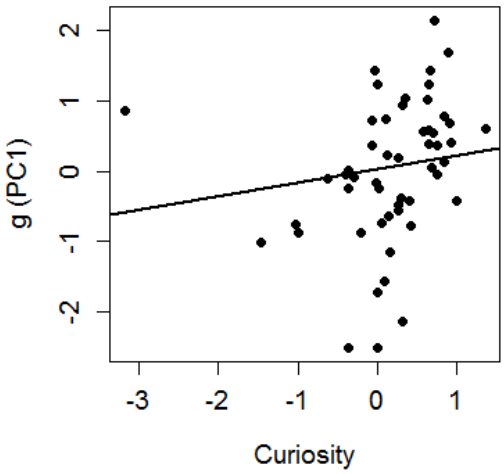
Supplementary Fig. S4: Tube Task with six tubes (L 37 x H 7.5 x D 6 cm). Subjects can use their fingers to reach trough the slot and to slide the bait along the tube. a) Wrong direction to slide the bait. Bait falls into the opaque trap. b) Correct direction to slide the bait. Bait can be retrieved out of the tube. c) Single tube, made out of metal with a transparent Makrolon plate to see the bait and run the finger in the slot. d) Complete test design, six tubes on a vertical board.



Supplementary Fig. S5: Visible Honey Tool Trap. a) Schematic view of the apparatus. Wooden box (H 80 cm x W 50 cm x D 7 cm) with two embedded transparent Makrolon tubes: a straight channel (L 30 cm x H 5 cm x D 5 cm) and a curved L-shaped channel [L 15 cm (10 cm until it bends down 5 cm), W 5 cm, D 5 cm]. b) Honey Tool Trap in its final version before use. c) Stick inserted in the curved channel to obtain honey (correct solution). d) Rope inserted in the curved channel in order to obtain honey (correct solution). e) Bornean individual using the stick on the apparatus.



Supplementary Fig. S6: Reversal Learning with 12 doors (L 13 cm, W 10 cm, distance to each other 15 cm). (a) Schematic view of the learning phase of the Reversal Learning. The subject learns the association of food and location (here right as an example). The association with location is enhanced with colors (here white). (b) Schematic view of Reversal Phase. The old association (right, white) does not hold any more. This time the reversed association (left, black) needs to be learned. c) Reversal learning board as it is presented to the individual. d) Sumatran subject conducting the reversal learning task by reaching through the bars and turning the doors.



Supplementary Fig. S7: The relation between curiosity and the potential *g* (PC1) plotted with a fitted line based on the LMM (Table 4) over all individuals (n=52). The outlier on the left was a highly uncurious wild individual.

CONDENSED CURRICULUM VITAE

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- Dissertation: "What makes orangutans intelligent? The Role of Experience and Learning in the Development of Problem-Solving Abilities in Orangutans"

Master in Biology at the University of Zurich — **02/2006 – 10/2007**
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Research associate — **05/2009 – 04/2012**
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Research associate — **10/2007 – 12/2007**
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FIELD EXPERIENCE

Team work, research management, scientific data collection, cultural adaptation

Orangutan Rehabilitation Station Nyaru Menteng of BOSF (Borneo Orangutan Survival Foundation)	**03/2014 – 06/2014** Borneo, Indonesia
Orangutan Release Site Danau Alo of SOCP (Sumatran Orangutan Conservation Program)	**02/2012 – 06/2013** Sumatra, Indonesia
Orangutan Quarantine Station Batu M'Belin of SOCP (Sumatran Orangutan Conservation Program)	**09/2012 – 12/2012** Sumatra, Indonesia
Orangutan Care Center and Quarantine of OFI (Orangutan Foundation International)	**05/2012 – 09/2012** Borneo, Indonesia
Chimpanzee Sanctuary Ngamba Island of CSWCT (Chimpanzee Sanctuary & Wildlife Conservation Trust)	**04/2011 – 06/2011** Ngamba Isl., Uganda
Orangutan Care Center and Quarantine of OFI (Orangutan Foundation International)	**06/2010 – 09/2010** Borneo, Indonesia
Wolfgang Koehler Primate Research Center Max Planck Institute for Evolutionary Anthropology & Leipzig Zoo	**05/2009 – 08/2009** Germany
Field site Tuanan in protected Mawas area of University of Zurich and the 'Universitas Nasional' in Jakarta	**02/2006 – 08/2006** Borneo, Indonesia

SCHOLARSHIPS & FUNDING

A.H. Schultz-Foundation – Winterthurerstrasse 190, CH-8057 Zurich **01-06/2016**

- Grant for PhD

CONFERENCE PRESENTATIONS

15th GFP – conference of the German Primate Society **15.-17.02.2017**
- Presentation and discussion "Is there general intelligence in orangutans?" Zurich, Switzerland

XXVI. IPS & ASP – Congress of the 'International Primate Society and the American Society of Primatologists' **21.-27.08.2016**
- Presentation and discussion "Determinants of Cognitive Performance in Rehabilitation-living Orangutans" Chicago, USA

6th EFP – Congress of the 'European Federation for Primatology' **25.-28.08.2015**
- Presentation and discussion "Determinants of Variation in Orangutans' Cognitive Performance I: Effects of Background and Housing Conditions" Rom, Italy

XXV. IPS – Congress of the 'International Primate Society' **11.-16.08.2014**
- Presentation and discussion "The Visible Honey Trap – Problem Solving in Orangutans" Hanoi, Vietnam

2nd EFP – Congress of the 'European Federation for Primatology' **03.-07.09.2007**
- Presentation and discussion „Planning in wild orangutans" Prague, Czech Republic

PUBLICATIONS

'Curiosity boosts orangutan problem-solving ability' — **in review**
L.A. Damerius, S.M. Graber, E.P. Willems, and C.P. van Schaik — (submitted 01/2017)

Journal: Scientific Reports — **01/2017**
'Orientation toward humans predicts cognitive performance in orangutans'
L. A. Damerius and S. I. F. Forss, Z. K. Kosonen, E. P. Willems, J. M. Burkart, J. Call, B. M. Galdikas, K. Liebal, D. B. Haun and C. P. van Schaik

Journal: Phil. Trans. R. Soc. B — **02/2016**
'The reluctant Innovator: Orangutans and the Phylogeny of Creativity'
C.P. van Schaik, J. Burkart, L. Damerius S. I. F. Forss, K. Koops, M. A. van Noordwijk, C. Schuppli

Journal: PLOS one, Volume 8, Issue 9 — **09/2013**
'**Wild Orangutan males Plan and Communicate Their Travel Directions One Day in Advance'** C.P.van Schaik, L.Damerius, K. Isler

Published conference abstracts:

Folia Primatologica, Vol. 79, No. 5, pp. 322-323 — **2008**
'Planning in the wild? A study of the cognitive abilities of wild orangutans (*Pongo pygmaeus*) at South Aceh, Sumatra, Indonesia.' Laura A. Damerius and Carel P. van Schaik

Folia Primatologica — **2015**
'Determinants of variation in orangutans' cognitive performance: I. effects of background and housing conditions'
L. A. Damerius, S. I. F. Forss, K. Z. Kosonen, J.M. Burkart, D.B. Haun, K. Liebal, J. Call, B.M. Galdikas, C.P. van Schaik

Folia Primatologica — **2015**
'Determinants of variation in orangutans' cognitive performance: II. influences of rearing conditions and human exposure'
S. I. F. Forss, L. A. Damerius, K. Z. Kosonen, J.M. Burkart, D.B. Haun, K. Liebal, J. Call, B.M. Galdikas, C.P. van Schaik

CO-AUTHORED PUBLICATION ABSTRACTS

The reluctant innovator: orangutans and the phylogeny of creativity

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Young orangutans are highly neophobic, avoid independent exploration and show a preference for social learning. Accordingly, they acquire virtually all their learned skills through exploration that is socially induced. Adult exploration rates are also low. Comparisons strongly suggest that major innovations, i.e. behaviors that have originally been brought into the population through individual invention, are made where ecological opportunities to do so are propitious. Most populations nonetheless have large innovation repertoires, because innovations, once made, are retained well through social transmission. Wild orangutans are therefore not innovative. In striking contrast, zoo-living orangutans actively seek novelty and are highly exploratory and innovative, probably because of positive reinforcement, active encouragement by human role models, increased sociality and an expectation of safety. The explanation for this contrast most relevant to hominin evolution is that captive apes generally have a highly reduced cognitive load, in particular owing to the absence of predation risk, which strongly reduces the costs of exploration. If the orangutan results generalize to other great apes, this suggests that our ancestors could have become more curious once they had achieved near-immunity to predation on the eve of the explosive increase in creativity characterizing the Upper Palaeolithic Revolution.

Wild Orangutan Males Plan and Communicate Their Travel Direction One Day in Advance

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Published in PLoS one September 2013

The ability to plan for the future beyond immediate needs would be adaptive to many animal species, but is widely thought to be uniquely human. Although studies in captivity have shown that great apes are capable of planning for future needs, it is unknown whether and how they use this ability in the wild. Flanged male Sumatran orangutans (*Pongo abelii*) emit long calls, which females use to maintain earshot associations with them. We tested whether long calls serve to communicate a male's ever-changing predominant travel direction to facilitate maintaining these associations. We found that the direction in which a flanged male emits his long calls predicts his subsequent travel direction for many hours, and that a new call indicates a change in his main travel direction. Long calls given at or near the night nest indicate travel direction better than random until late afternoon on the next day. These results show that male orangutans make their travel plans well in advance and announce them to conspecifics. We suggest that such a planning ability is likely to be adaptive for great apes, as well as in other taxa.